Neuron, Vol. 24, 95–104, September, 1999, Copyright ©1999 by Cell Press

The What and Why of Binding: The Modeler's Perspective

Review

Christoph von der Malsburg*
Institut für Neuroinformatik
Ruhr-Universität Bochum
44780 Bochum
Federal Republic of Germany
University of Southern California
Los Angeles, California 90089

In attempts to formulate a computational understanding of brain function, one of the fundamental concerns is the data structure by which the brain represents information. For many decades, a conceptual framework has dominated the thinking of both brain modelers and neurobiologists. That framework is referred to here as "classical neural networks." It is well supported by experimental data, although it may be incomplete. A characterization of this framework will be offered in the next section.

Difficulties in modeling important functional aspects of the brain on the basis of classical neural networks alone have led to the recognition that another, general mechanism must be invoked to explain brain function. That mechanism I call "binding." Binding by neural signal synchrony had been mentioned several times in the literature (Legéndy, 1970; Milner, 1974) before it was fully formulated as a general phenomenon (von der Malsburg, 1981). Although experimental evidence for neural synchrony was soon found, the idea was largely ignored for many years. Only recently has it become a topic of animated discussion. In what follows, I will summarize the nature and the roots of the idea of binding, especially of temporal binding, and will discuss some of the objections raised against it.

Classical Neural Networks

Classical neural networks were developed as models of brain function. In developing these models, several questions needed to be addressed:

(1) How are brain states to be interpreted as representations of actual situations? In other words, how is neural activity interpreted as a neural code, or, in computer parlance, as a data structure?

(2) What is the nature of the mechanisms by which brain states are organized?

(3) In what format is information laid down permanently in the brain?

(4) How is memory laid down? In other words, what are the mechanisms of learning?

The questions remain open, but, as we shall see, plausible answers have been offered by classical neural networks. Interestingly, in the context of the field of Artificial Intelligence, no general answers to these questions are provided, in the conviction that specific problems need specific data structures and specific algorithms (or, in our parlance, mechanisms of organization). Neuroscience and neural modeling, on the other hand, have the ambition to find general answers. It is this commitment to generality that results in the binding problem being a fundamental feature of the neural code.

The Psychological Moment

Before discussing the answers to the above questions that are postulated by classical neural networks, it is important to introduce an important parameter. Although not often made explicit, it is important to fix a temporal scale *T*, which we will refer to as the "psychological moment" (in the sense of "short period"). At times shorter than *T*, one speaks of mental state or brain state, whereas at times greater than *T* one sees a succession of states or a "state history." Whereas state history is subject to conscious scrutiny (that is, it potentially gets reflected in all modalities—memory, language, etc.), no such conscious analysis is possible below *T*. State history is ignored by most or all models, and the conceptual disagreement about the binding issue focuses exclusively on the definition of state, that is, on times below *T*. It is difficult to pin down a definite value for *T*, but a plausible range may be from 50 to 200 msec. Regardless of the exact value, it is important to realize that the arena for the discussion of the binding problem is at a time scale less than *T*.

Classical Neural Networks: Answers to the Issues of Brain Function

Classical neural networks are described by a deeply engrained set of concepts, often attributed to Hebb (1949) and Hayek (1952) but in reality much older, which give definite answers to the questions 1–4 above.

(A) The neural code: neurons are taken as concrete symbols, as semantic atoms. They can be interpreted in relation to patterns and events external to the organism. Neurophysiology has provided a solid experimental basis for this statement, although some extrapolation is needed to extend it to all neurons in the brain. The interpretation of neurons as semantic atoms is generally accepted and is not the matter of much dispute. However, the following addition will have to be a focus of our discussion:

(A′) A neuron has only one degree of freedom for a given psychological moment: it is either on or off (or it is on to a certain degree). Thus, the brain state is described by a list—or vector—of neural activities. In order to know what the brain is about in a given psychological moment, it is only necessary to know this vector, as well as, of course, a description of the symbolic meanings of all neurons. This interpretation of brain activity deliberately ignores the fact that actually recorded neural signals are not constant in any sense over *T*—or over any fixed time scale, for that matter. It is rather maintained that the observed microstate history is inconsequential for the function of the brain.

(B) The mechanism of organization of brain states is based on the fluxes of excitation and inhibition, a neuron collecting incoming signals and firing when a threshold is surpassed (see, for instance, the switching rule of McCulloch and Pitts [1943]). The dynamics of the system

---

*E-mail: malsburg@usc.edu.

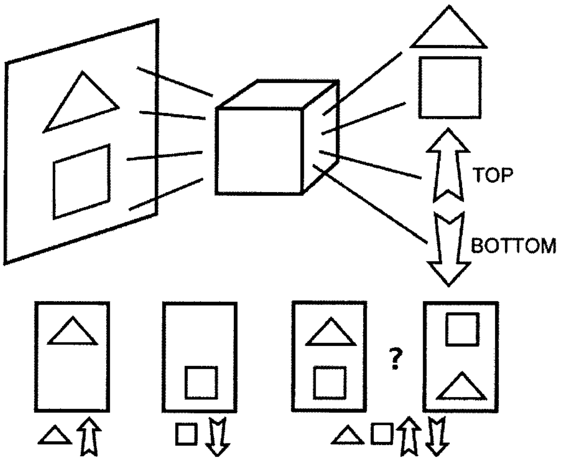

Figure 1. Rosenblatt's Example

See text for explanation.

is regulated so that it stabilizes activity within the psychological moment. (In associative memory models, this is, for instance, achieved by requiring connections between any pair of neurons to be symmetric, with the consequence that the system displays attractor dynamics.) Without this restriction, a McCulloch and Pitts system would be a general digital machine without any inherent tendency to organize, kept on track only by the force majeure of a programmer with detailed insight into the switching process.

(C) Long-term memory is stored in terms of synaptic weights.

(D) Long-term memory is laid down by mechanisms of synaptic plasticity, based on the statistics of neural signals, especially their temporal correlations.

These postulates will be referred to as the framework for "classical neural networks." It forms the conceptual basis for a large and important part of current neurosciences, especially for the genre of brain modeling usually referred to as Neural Networks or Connectionism. Since existing neural models cover only a small range of the brain's functional repertoire, an all-important issue is whether the above framework constitutes an adequate basis from which to conquer the rest solely by constructing appropriate specific wiring diagrams and control parameters.

The Binding Problem

It has been argued that the classical code of neural networks is very poor, too narrow in its possibilities to serve as a basis for an expansion of the functional range of current brain models (von der Malsburg, 1986; Fodor and Pylyshin, 1988). The underlying weakness is best illustrated by a classic example due to Frank Rosenblatt (1961): imagine a specific neural network for visual recognition, which is internally structured such that it can derive four propositions and represent them by output neurons. Two neurons recognize objects, a triangle or a square, both generalizing over position. The other two indicate the position of objects in the image: in the upper half or in the lower half, both generalizing over the nature of the object (see Figure 1). When showing single objects to the network it responds adequately, e.g., with (triangle, top) or (square, bottom). A problem arises, however, when two objects are present simultaneously. If the output reads (triangle, square, top, bottom) it is not clear whether the triangle or the square is in the upper position. This is the binding problem: the neural data structure does not provide for a means of binding the proposition top to the proposition triangle, or bottom to square, if that is the correct description. In a typographical system, this could easily be done by rearranging symbols and adding brackets: [(triangle, top), (square, bottom)]. The problem with the code of classical neural networks is that it provides neither for the equivalent of brackets nor for the rearrangement of symbols.

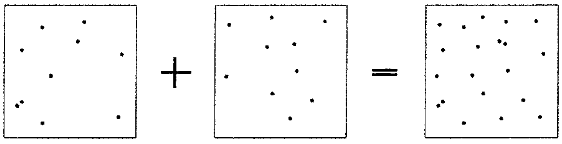

Figure 2. The Superposition Catastrophe

If two sets of active neurons (left and middle panel) are simultaneously activated (right panel), information on their membership in the original sets is automatically lost.

This is a fundamental problem with the classical neural network code: it has no flexible means of constructing higher-level symbols by combining more elementary symbols. The difficulty is that simply coactivating the elementary symbols leads to binding ambiguity when more than one composite symbol is to be expressed. Let's assume it was vital for an organism to trigger some action in response to a triangle if it was in an upper position but not in a lower one. The reaction would then have to be tied to the coincidence of activity in cells (triangle) and (top), which, however, would also occur if the triangle were at the bottom and a square at the top. The animal therefore would respond to a so-called false conjunction, perhaps with grave consequences. An analogous situation occurs in the brain. Correspondence between object type and position is explicit on the retinal level. Its loss on the way to the output of the circuit is due to the generalization that is taking place within the circuit: for instance, in the brain's "what" and "where" pathways in the temporal and parietal pathways of primate cortex.

This problem is a general one, with implications far beyond that of vision. Imagine a mental object that is represented by the set *P* of neurons (refer to Figure 2) and another mental object represented by set *Q* (possibly overlapping with *P*, but that is not a point here). Now it becomes important to activate both objects in the same mental operation (when, for instance, comparing them). What would be more natural than to coactivate both sets in the same brain state? Such coactivation, however, leads to what we call the "superposition catastrophe": the two sets will merge into one, and the neural code will not express the information needed to subdivide the composite state into its components (see Figure 2).

Combination Coding as a Solution to the Binding Problem

Rosenblatt's problem has a simple solution in terms of combination-coding cells. It would suffice if there existed a neuron that reacted to a triangle in the top position (or to a set *P* or *Q* of neurons). This could be realized with the help of connections from the lower, elemental levels, on which generalization has not yet taken place. However, a problem arises where appropriate combination-coding cells do not exist or cannot exist (due to the impracticality of the large numbers required, or to the previous history of the system) and where there are connection patterns that could cause confusion. The assumption that combination coding cells are available when and where required is problematic when the system to be modeled is a general purpose device.

Most symbol systems have means of combining elementary symbols into more complex ones, which can then be handled as units without danger of ambiguity and which have explicit structure on the basis of which they can be compared, recognized, decomposed, and further combined to build even higher structures. That the classical code of neural networks doesn't have such means is the root of the binding problem. It is a very curious proposition that the brain, the ultimate handler of symbol systems, shouldn't have a general mechanism for combining subsymbols. Other symbol systems (such as mathematics or natural languages) suggest that more complex binding patterns may be required than just grouping a number of elements into one block with no internal structure. The visual image of an extended object may need to be represented as an array of local features that are bound together in a way that expresses the topological neighborhood relationships within the figure or even a hierarchy of object parts (Biederman, 1987); similarly, the representation of natural language structures requires binding arrangements with hierarchical structure.

Why not have a purely hierarchical system of combination-coding cells? There may be good reasons that certain combination-coding cells should not exist. The more complex the combination a cell represents, the more special the context to which it refers. Any experience gained in a particular context (and recorded in terms of changed synaptic connections) should be affixed to the most general description of the situation, so it can be exploited in other contexts. If, for instance, something was associated with the appearance of a triangle that just happened to be in an upper position, it would be inefficient to affix the association only to an upper-triangle cell, for then the experience would have to be repeated and relearned for all positions of the triangle. In a similar vein, the *absolute* location of a speck of ink on paper is of very little relevance; what counts is its *relative* location in a pattern. Our environment is complex because it is combinatorial: complex objects and situations are constructed by combining simpler elements. To try to represent this complexity in a noncombinatorial way, letting single cells stand for external objects of any complexity, appears to be a terribly inefficient strategy. Any combinatorial symbol system, however, needs a mechanism to bind elements into groups.

Some evidence exists that suggests that the brain does not simply use combination-coding cells to process stimuli. Psychophysical studies show that under certain conditions the brain's binding mechanism may fail, and people will report "illusory conjunctions" (see Wolfe and Cave, 1999 [this issue of *Neuron*]). When given enough viewing time, subjects do not commit such "false conjunction" errors. In a related vein, conjunction search experiments (Treisman and Gelade, 1980), in which subjects are asked to find an object with a specific combination of features in an array of distractors with one of those features each, show that reaction times scale linearly with the total number of elements in the display. From these types of experiments, one can conclude that relevant combinations of features are not represented by combination-coding cells and that the brain requires time to form or ascertain the correct bindings.

Are Classical Neural Networks Universal?

There is a widespread opinion that classical neural networks are a universal medium with no limits to their abilities and that consequently they are not subject to the binding problem. I will address this claim in two steps. First, I will discuss whether universality suffices as a solution to the brain's problems and then I will raise doubts as to whether classical neural networks are indeed a universal medium.

The idea of universality was crystallized with Alan Turing's formulation of the Turing machine and his demonstration that no effective procedure can be conceived that cannot be realized as the program of a Turing machine. Thus, any completely specified function can be realized as a program, or algorithm, run on a computer, the only limits to this being storage space and time. From this, it was extrapolated that mental processes, if only made concrete in terms of rules, could be realizable in machines. Under this view, the brain is a digital machine and has the same universality as the computer or the Turing machine, if only sufficiently many neurons are available. McCulloch and Pitts (1943) applied this idea to modeling of the nervous system, proving that any logical function can be realized as a network of threshold elements if they are appropriately connected.

But what does universality buy? It can be compared to the universality of a pen and sufficiently many sheets of white paper as a universal medium for formulating novels. You still have to write them. Over time, the field of Artificial Intelligence discovered that it is not a practical task at all to write a program that emulates the capabilities of the brain. It is becoming increasingly clear that the only goal we can hope for is to establish a system that constitutes a basis for self-organization and learning, as the equivalent of a newborn, or better still, the genetic program for the development of a brain, and to let it learn from experience and from communication with others.

Brain theorists realized this in the late 1950s and modified McCulloch and Pitts' networks to accommodate self-organization and learning. The resulting framework of classical neural networks has a tendency to fall into stable patterns and learns by synaptic plasticity. However, these changes may have come at a price: it is not clear whether neural networks are universal in any sense, although the community seems to have inherited the implicit belief that they are and that any brain function can be modeled on the basis of those few abstractions from the real nervous system that went into the formulation of neural networks. It is not even clear how to formulate a new universality theorem. Classical universality states, "give me a procedure and I'll tell you how to implement it." The neural network version of universality would have to be, "give me a brain problem and I will be able to implement it in classical neural networks." But how can we characterize brain problems in any general and satisfactory way? It would be foolish to argue that "this is a particular problem I have solved on the basis of classical neural networks, which proves that all of them can be solved this way."

In the context of the present discussion, the particular version of universality that some critics of the binding problem uphold, is "state a concrete problem, and I will solve it with a classical neural network without ever running into a binding ambiguity." The common argument to support this posits that any binding ambiguity implicit in a stated problem can be dealt with by the concrete combination-coding cells in the model network that solves it (for example, see Riesenhuber and Poggio, 1999a [this issue of *Neuron*]). A concrete example of this approach is Mel and Fiser's model (1999) for recognizing words from text. The network codes text in terms of triplets of contiguous letters and is based on the statistical observation that in English no two words agree in all their letter triplets. Thus, in this special case, the model completely avoids the binding problem and ensuing compositional ambiguity that would beriddle a model based on a representation by single-letter cells only.

Although such examples are meant to support a general universality claim, it is very doubtful that such a claim can ever be established. It is too easy to state problems that are far beyond the abilities of present neural network models. Just think of the task, "emulate the human ability to segment visual scenes, with all the necessary cue integration." Although the problem is old, there exists no classical neural network solution to it, and perhaps for good reason.

Binding by Temporal Synchrony

How could binding be implemented in the brain? The basic idea of temporal binding is that signals of neurons that are to be grouped together are correlated in time. Neural signals can thus be evaluated in two ways: one of them is the classical concept of neural firing rate, in which the relevant parameter is the running average of the number of spikes arriving within any period T. The second concerns temporal correlations of signal fluctuations happening on time scales faster than T, and it is these correlations that express binding. The subdivision of the time scales above and below T is on final account arbitrary (unless one sticks to the distinction that changes slower than T are accessible to introspection while faster changes are not). Pick a scale T, and then evaluate signal fluctuations below T in terms of correlations, while calling fluctuations above T rate changes (there is, of course, a lower bound, that depends on the fastest temporal scale that can be processed by neural tissue). For the brain, T is related to the psychological moment, ill-defined as it may be, so we will take T to be of the order of 50 to 200 msec (although scales up to minutes and beyond are also of potential relevance). Throughout this discussion, I discuss signal correlations as if they were to be evaluated without taking into account relative delays. However, it may be necessary to also consider delayed coincidences as argued in Bienenstock (1995).

To understand the general idea of temporal binding, the exact nature of the signal fluctuations is not relevant. There has been much discussion over the experimental evidence concerning whether oscillatory signals are or are not important in this respect, but that discussion is a side issue that shouldn't cloud the more fundamental question of whether binding is a problem and whether neural signal correlations are a solution to that problem. Although much of the discussion of signal correlations focuses on the binary case, the correlation of just two neurons, it should be emphasized that the much more relevant and important type of event concerns correlations of higher order: the simultaneous firing of larger groups of neurons. The reason is this: for correlations to play an important role in the brain it must be possible for them to be evaluated quickly and reliably. Since for any given set of impulses there may be accidental coincidences, it is vitally important to discern true correlations from noisy background. For binary correlations, this is only possible for long observation times, but for correlations of sufficiently high order, even individual coincident events can become highly significant.

With regard to the plausibility of temporal binding, there are the several fundamental questions that need to be discussed:

(1) How do correlations in temporal signal structure arise? Ultimately, the purpose of temporal binding is to express significant relations between data items, e.g., of causal or spatial nature; the physical interactions establishing such relations must be represented by signal correlations. Since many of these interactions are already present in the external world, temporal correlations can be imposed by external stimuli triggering the neural signals. That this happens with causally related external events is evident, but it is less often realized that the same can be due to our own bodily and eye movements, which create a stream of sensory impressions whose temporal structure expresses spatial structure of the environment. Thus, some of the signal correlations relevant for binding are already implicit in the perceptual input (see also Singer, 1999b [this issue of *Neuron*]).

As a short aside, the argument is often raised that the use of temporal patterns for expressing binding may clash with the use of temporal patterns for other purposes, such as the representation of temporal structure as given in the external world. This is especially relevant to the auditory, language, and motor modalities. This clash may be avoided by the nervous system by recoding temporal signals into a format that does not involve rapid signal changes. Single neurons responding to and representing syllables would be an example of this.

More correlations (probably the overwhelming majority) are created within the nervous system by synaptic connections. If neuron a fired neuron b, the signals of the two would be correlated (disregarding a small delay). Correlations induced by synaptic connections also signify causality. In addition, activity in neurons without connections between them but with connections from a common input can be correlated. In the Rosenblatt example, the binding problem could be solved if the neurons in V1 that are activated by a triangle in a given position pass the temporal signature of their signals on to neurons expressing shape identity on the one hand

and position on the other, such that those signals came to express their common origin.

(2) How are signal correlations evaluated in the brain? If two action potentials arrive at a common target neuron, their relative timing exerts a strong influence. If signals arrive simultaneously, they can cooperate to raise the neuronal membrane potential above firing threshold. If, however, they miss each other in time, so that the effect of the first impulse has decayed before the second arrives, they might both fail to fire the target neuron. Thus, neurons act as coincidence detectors and do evaluate signal correlations (Abeles, 1982b; Marsalek et al., 1997). The exact details of this interaction depend upon many complex factors, including membrane time constants, nonlinear effects, and dendritic geometry. In consequence, current neurophysiology cannot solidly predict the temporal resolution at which spike coincidences are evaluated; however, a likely range is 1–10 msec.

If all correlations were to be evaluated globally by single neurons, a combination-coding cell would be required for each binding pattern, defeating the purpose of binding. However, complex correlation patterns created by a circuit of interconnected neurons can be evaluated by other circuits of appropriately interconnected neurons, each individual neuron checking only a small subpattern. Thus, pairs of circuits may or may not resonate with each other in terms of the correlation patterns that they produce. This point is probably most easily understood with reference to the concrete models of invariant object recognition that are discussed below.

It was proposed (von der Malsburg, 1981) that correlation patterns are also evaluated by rapid reversible synaptic plasticity (in addition to slow plasticity). A connection that is physically present and would cause confusion in a given situation could be temporarily inactivated when activity on both the presynaptic and postsynaptic side is sensed, but is uncorrelated. Confusion could thus be suppressed in the given situation, even if the signals involved were to develop stray coincidences, until the switched-off connection returned to near its previous value on the time scale of seconds or minutes.

(3) How can correlation patterns be effective on physiological timescales? If they are to play a role in the brain's function, it is mandatory that they be evaluated within short time intervals. Finding a pair of correlated neurons in a set of others firing stochastically may take unrealistically long integration times. The situation can be improved in two ways. As previously mentioned, one way relies on coincidences of high order. Even when superimposed on stochastic signals, a single event of *n* simultaneous spikes, with *n* large enough (say, 50 or 100), can be of high statistical significance. The other way relies on the suppression of accidental correlations by appropriate inhibitory circuits. Thus, if a large set of neurons needs to be subdivided into several bound subsets, inhibition between the subsets can make sure that no coincident spikes between neurons in different subsets occur at all. This is an integral part of many models, e.g., von der Malsburg and Buhmann (1992) or Wiskott and von der Malsburg (1995).

(4) How are the network patterns created that are required for the production and evaluation of significant firing patterns? Random connection patterns will neither be able to create significant firing patterns nor be able to distinguish them. Many of the arguments raised against the validity of the idea of temporal binding, e.g., Shadlen and Newsome (1995) and Shadlen and Movshon (1999 [this issue of *Neuron*]), are implicitly or explicitly based on the assumption of random connectivity. If, however, the nervous system is endowed with the capacity to self-organize using synaptic plasticity of slow (von der Malsburg and Singer, 1991) or fast (von der Malsburg, 1981, 1985) time scales, attractor networks will form that are able to support significant correlation patterns and that are in turn stabilized by exactly those correlation patterns. For examples see below.

(5) How can the signal correlation patterns that express binding relations be found experimentally? One could well imagine that the brain's function could be dominated by well-organized correlation patterns and yet that available experimental techniques could be unable to reveal them. If the essential patterns were of high order, say 100, and occurred only a few times in any given stimulus situation, it would be difficult with only a few electrodes to ascertain their existence. Even using many electrodes at a time, one could be reduced to blind search, as neither the circuits producing the relevant correlations nor the circuits evaluating them would be known. Just finding correlation patterns, even if their occurrence is context dependent (Abeles et al., 1994; Bair and Koch, 1995; Buračas et al., 1998), proves that the brain can reliably process temporal patterns but does not prove their relevance to the binding issue.

Another fundamental difficulty for the experimental verification of binding correlations may be created by a tendency of the nervous system to produce correlations (or rather decorrelations) only where needed to disambiguate a situation and suppress false conjunctions. As soon as the network had reacted to the signal by switching off the connections that would create confusion, signal correlations could disappear again without any further functional consequences. As psychophysical or neurophysiological experiments tend to stress repetitions of stimuli within narrowly defined experimental paradigms, most of the signal patterns relevant for binding may be gone after the initial training or set-up period. However, if we are lucky, nature will extend the grace of producing low-order correlations that moreover could be interpreted functionally on the basis of applied stimuli. Figure-ground separation may be a unique experimental opportunity, as the required binding pattern is very simple—requiring just distinction of the figure from the ground, which should be expressed by the creation of correlations between neurons within the figure and suppression of correlations between neurons within the figure and those within the ground. Because each new stimulus may be a unique combination of local cues, the nervous system probably cannot suppress erroneous conjunctions by permanently adjusting circuits.

Beyond Temporal Binding

In one extreme and untenable view, all of the thalamocortical apparatus would be a collection of cells with rather low-level meaning, defined since birth by their efferent or afferent connections, and all higher-level symbols would be constructed as temporal correlation patterns, supported by appropriate connectivity patterns. This view is untenable for several reasons. First, experimental results have revealed neurons with rather high-level and specialized symbolic meaning. However, a more fundamental reason is the rather limited temporal resolution of neural signals that can be processed by cortical circuits. The exact value of this resolution is at present a matter of contention, but hardly anybody would argue it lies far outside the range 1 to 10 milliseconds. The ultimate reason for this limitation is probably not to be found in neural membrane properties but rather in the temporal spread of signals over various pathways between one point and another. Thus, the capacity of the system for expressing binding patterns within the psychological moment is very limited, and the amount of binding ambiguity that a network can tolerate is correspondingly small. Consequently, there must be other mechanisms at work in the developing and learning brain that reduce binding ambiguities as they arise. What could such other mechanisms be?

So far, the only one seriously studied in the context of classical neural networks relies on combination-coding cells. These are to represent meaningful subpatterns and have to dominate the system such that meaningless subpatterns do not evoke a response. In Rosenblatt's example, a cell that is to represent "triangle on top" must have appropriate connections that let it fire only if indeed a triangle is shown on top, and its activity must be a *necessary* condition for any reaction to triangle-on-top, that is, simultaneous activity from a triangle cell and a top cell must be prevented from eliciting such reactions because they could constitute a false conjunction. As soon as such wiring is in place, temporal binding is relieved of the necessity to keep the now-represented subpatterns apart, and the binding problem for this particular context has vanished. The importance of temporal binding lies in the fact that it is a ubiquitous medium that steps in wherever a situation requires a binding distinction for which those other means are not, or not yet, in place. In these cases, temporal binding can bring out structural information that is implicit in the connectivity acquired previously and in the input. However, ultimately, binding structures must be off-loaded to other mechanisms before the capacity of temporal correlations is surpassed.

Many scientists view focused attention as an alternative to temporal binding (see Reynolds and Desimone, 1999 [this issue of *Neuron*]). Focal attention is a mechanism to functionally suppress stimuli that do not belong to the theme of current interest and to activate those that do. Attention acts in a sequential manner—we can attend to only one thing at a time. Thus, attention is a mechanism of temporal binding, although on a time scale longer than the psychological moment. The reason there is so much agreement about the existence of this form of temporal binding, which acts on the scale of large fractions of a second or longer, is that the different time slices are open to scrutiny, both via introspection, and externally, by way of a person's actions, words, and eye movements. It seems plausible that temporal binding on the one hand and attentional mechanisms on the other are just two points on an uninterrupted continuum. Local circuits have their own "attentional mechanism," flashing from one microtopic to the next, although at a sequence too fast for distant parts of the brain to follow. In order to couple larger areas of the brain, slower time courses are required (due to longer and more widely spread transmission delays), but the coupling mechanisms very likely are of the same nature.

Importantly, the mechanism of temporal binding can serve as the basis for rapid, and in the extreme case, single-trial learning of the connections required for the circuits to replace it. Since evidence for the combinations of cells to be represented is produced in the form of correlations, combination-coding cells can be formed quickly by synaptic plasticity (if the plasticity mechanism is sensitive to the fine temporal structure implicit in temporal binding, a condition called "refined synaptic plasticity" in von der Malsburg [1981]). Single-trial learning on this basis was demonstrated in Konen and von der Malsburg (1993) and represents a great potential that yet has to be fully exploited. This is in sharp contrast to conventional neural network learning, which is based entirely on evidence implicit in the statistics of consecutive stimuli and is therefore much slower. (For neurophysiological evidence supporting refined plasticity, see Singer, 1999b [this issue of *Neuron*]).

It is very unlikely that all binding structures can be represented by combination-coding cells. The arrays of point-to-point correspondences that bind the image of an object to a stored model (Wiskott and von der Malsburg, 1995) may be an example for which it would be difficult. Perhaps the brain has at its disposal other mechanisms by which ordered arrays of bound representations can be stored and quickly retrieved as connectivity patterns. The logical structure of such a mechanism has been worked out (von der Malsburg, 1985; Bienenstock and von der Malsburg, 1987), but that implementation still relied on temporal synchrony for activating stored connectivity patterns and thus is slow. If there were mechanisms in the brain by which connections could directly excite or inhibit each other, fast retrieval of associatively stored connectivity patterns could be realized. Several authors have proposed the existence of connector cells (Dev, 1975; Sejnowski, 1981; Phillips et al., 1988), to implement rapidly varying circuits. A connector cell can be excited or inhibited like any other neuron, but its sole purpose is to represent and control the connection between a fixed pair of other neurons. Connector cells could be the basis for the rapid activation of connectivity patterns. However, as their signals cannot easily be interpreted in terms of concrete symbolic meaning, they would amount to a somewhat wasteful use of neurons, and their expected anatomy wouldn't correspond to any of the known cell types in the brain. In addition, it would be desirable to have a clear picture of how appropriate connector cells could develop ontogenetically.

Another important proposal for implementation of quickly variable connection patterns in the brain is based on presynaptic control of connections (Anderson and Van Essen, 1987) or three-terminal devices (Hinton, 1981). According to the idea, command neurons can switch on individual connections or whole connection patterns. Anderson's "shifter circuits" set up precise one-to-one connections (or rather a cascade of such connections) between primary cortices and area IT. As with the connector cells, one difficulty with this proposal is the lack of a clear picture of how the correct control could be put in place, that is, how information about the quality of match between potential correspondence points could be communicated to the control neurons, or how these circuits could come about ontogenetically. Clearly, more theoretical work is needed here on all sides. What is needed is to develop a theory describing how binding patterns are first "discovered" by the circuit with the help, for instance, of a temporal correlation mechanism on the basis of pattern similarities and are then "burned into the network" as reliable and quick-to-retrieve connection patterns, not requiring further time-consuming signal correlations. Temporal binding would therefore only be necessary in the first stage of discovery, when no appropriate binding circuits are yet in place.

If indeed temporal binding were nothing but a makeshift means for the nervous system to solve binding problems as they unexpectedly turned up, and if they would always be quickly obviated by the system by appropriate changes to the network, it would be very difficult to find evidence for binding experimentally: one would have to set up series of one-time experiments, as has been proposed in Triesch and von der Malsburg (1996). On the other hand, certain binding problems cannot be made to go away and will always require temporal signal structure. It is very likely that sensory segmentation is one such problem, which would then lend itself well to experimental demonstration of the mechanism of temporal binding. Repeating experiments of the Gestalt psychologists with behaving animals, where a clear correlation was demonstrated between psychophysical grouping on the one hand and the occurrence of signal correlations in the relevant cells on the other, would convince the last doubter.

Applications

The original proposal for a general binding mechanism (von der Malsburg, 1981) arose from the attempt to solve a number of conceptual problems that stood in the way of understanding important functional aspects of the brain on the basis of neural models. One form of evidence that would argue for the existence of a binding mechanism in the brain should therefore come from visible progress with those conceptual problems. In my own experience, the assumption of the existence of a binding mechanism removes a major roadblock and leads to the dissolution of many formerly difficult problems.

Coarse Coding of Multiple Representations

One problem in brain function is how to represent an entity that is described by a number of parameters. One possible way of doing so would be to create a space with as many dimensions as there are parameters and to fill that space with neurons, allocating one neuron for each possible combination of parameter values. For instance, to describe a small object in terms of retinal position, stereo depth, velocity, and color would require eight dimensions (not counting parameters to describe the object's shape). Unfortunately, this is a very expensive proposition, as with N dimensions and M values to be distinguished per dimension, the number of neurons required would be M^N. With $N = 8$ and $M = 5$, this would be almost 400,000 neurons. With coarse coding, on the other hand, that same space is defined by using neurons to fill not the entire volume but only the axes. Thus, in the case above, one would need $M + N = 40$ neurons only. An individual entity would then be represented with the help of N neurons, each one specifying a value for one of the parameters.

If only one item were present at any given time, this would be a perfect solution. If, however, several entities must be represented at the same time, the binding problem arises, as those neurons that refer to one entity need to be bundled to avoid conjunction errors. Thus, the availability of a binding mechanism makes coarse coding possible. It seems impossible to use coarse coding without a binding mechanism, and many functional models, as those discussed below, cannot well be realized without coarse coding.

Sensory Segmentation

Another important application of binding—in the eyes of many, *the* application of binding—deals with the segmentation problem of perception. In all sensory modalities, natural stimuli are a mixture of signals that originate with independent sources in the environment. Examples of this include the cocktail party problem of keeping track of individual voices in the hubbub of a social environment, and in the visual modality of separating images of individual objects from one another before any one of them can be separately recorded or recognized. Segmentation is a classical binding problem, as individual neural signals need to be bound together so they can be handled as units corresponding to whole objects or coherent stimuli. The difficulty in solving the problem lies in the fact that a number of different subcues need to be integrated with each other to yield reliable segmentation. In the visual modality, for instance, relevant subcues are motion, color, texture, stereo depth, coherent edges, and simple or known shapes. Any one cue on its own is unreliable. Simple filter mechanisms ("suppress all points for which cue x doesn't have value y") therefore break down in natural scenes.

Concrete models have been presented that express sensory segmentation by signal correlations and anticorrelations (see for example von der Malsburg and Schneider, 1986; Wang et al., 1990; Sporns et al., 1991; von der Malsburg and Buhmann, 1992; Eckes and Vorbrüggen, 1996). Except for one model (von der Malsburg and Schneider, 1986), which was based entirely on temporal structure already in the input, all these models rely on permanent excitatory connections between cortical neurons to encode the likelihood for them to be activated by the same figure. These connections reflect the Gestalt laws of perceptual grouping. Thus, for example, two neurons should have a connection if they correspond to similar local features (e.g., color, texture, or stereo depth), although they occupy different locations in the visual field. Similarly, two neurons should excite each other if they correspond to the same location in the input space, reflecting the fact that most of the time a location is occupied by a single object. In addition, two neurons should be connected (indirectly or directly) if they are part of a familiar pattern. According to one particular model (Wang et al., 1990), this latter rule is the sole basis for the ability of our olfactory system to parse a composite odor into known components, the necessary connections having been previously learned via associative memory.

In all these models, the combined action of all excitatory connections is to bind the neurons that are activated by the same figure into one composite whole, by synchronizing their activity in time. Inhibitory connections are used to suppress simultaneous activity in cells belonging to figure and ground, thus making the signal correlations within figure and within ground stand out unambiguously, and minimizing accidental coincidences. The excitatory connections necessary for segmentation might in large part be established by plastic processes as the result of previous experience with perceptual segmentation, although the synaptic plasticity must surely be boot-strapped by innate structure. All the different excitatory connections in the system conspire to create global correlations within a figure (or ground), and this fact is a natural basis for the subcue fusion that is necessary for segmentation in natural environments. It has been shown that natural visual input can be segmented with pixel accuracy with the help of subcue fusion based on a binding mechanism (Eckes and Vorbrüggen, 1996; Adam, 1998).

At least in the visual and auditory modalities, it cannot be expected that all necessary excitatory connections be realized within the primary areas, V1 or A1. Although it is not necessary for connections to span a whole figure globally to create the required correlations, it is still necessary to bridge gaps produced by partial occlusion of a figure. Also, some of the relevant features are not even computed within primary cortex. Thus, color and motion processing require participation of areas V4 and MT. Also, the cue of familiar form presumably requires a detour to infero-temporal cortex, where known forms are stored. Back projection from there to the primary cortices is necessary to combine low-level and high-level information, since both types of cues on their own would in many situations not be able to disambiguate complex visual stimuli. That back projections from higher to lower levels seem to lack the necessary precision is an issue that I will address below.

As for the expected time course of signals that express binding of all parts of a figure to each other, it is not necessary to require simultaneity from one end of the figure to the other. This would only be required if a single neuron were to evaluate the figure as a whole, which is unlikely to ever happen in the brain. If a figure is evaluated by individual neurons only in terms of (overlapping) local subpatterns, what is necessary is that signals be fairly synchronous within the subregions defining those patterns. On the global level of the figure, signals have to be coherent, but the timing of events may drift from one end of the figure to the other in a continuous fashion.

Invariant Object Recognition

Invariant representation and recognition of objects and patterns is one of the fundamental functions of perception. Invariance is required to link the infinite variety of sensory patterns that may be created by any one external object or process to an individual representation. In vision, this variety of sensory patterns is due to differences in retinal position, size, orientation, perspective, object deformation, illumination, background, partial occlusion, surface reflections, noise, and other parameters. Many theories of vision assume that invariance is achieved via decomposition of sensory patterns into elementary features, which are represented by individual neurons that then connect to invariant feature cells by "feature type-preserving connections." Thus, an invariant cell receives connections from the cells of the same feature type in all different locations (or whatever the parameter to be generalized might be). A binding problem arises from such a structure, for since generalization is performed independently for each feature, information about relative position, size, and orientation is lost. For a given set of feature types, this lack of information can lead to the inability to distinguish between patterns that are composed of the same set of features, though in different relative positions, sizes, or orientations.

The conflict between generalization and unambiguous feature relations can be resolved with the help of temporal signal correlations that are created on an early level of processing where feature relations are still explicit. Different spatial arrangements of features in the input layer thus lead to different binding patterns between the features involved. These binding patterns can be

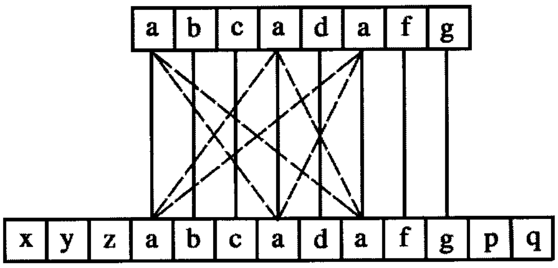

Figure 3. Invariant Pattern Recognition by Dynamic Link Matching

A visual input pattern is represented in the primary areas of visual cortex as an array of local features, symbolized by the lower row of letters. It is to be recognized on the basis of its isomorphy to one of many patterns stored in secondary cortex (perhaps area IT), symbolized by the upper row of letters. The two domains are connected by feature type-preserving connections. As the presented figure can vary in position (and other parameters), an invariant feature cell in secondary cortex must have connections from cells for the same feature type in all positions (and other variants) in primary cortex. This is indicated just for the feature "a," which occurs repeatedly in the figure. Only a subset of these connections run between corresponding points (solid vertical lines). These connections are distinguished by the fact that they form a consistent system connecting neighboring (and synaptically coupled) points on one level to neighboring points in the other. Others form a haze of false correspondences (dashed lines). During a recognition process, wrong correspondences are suppressed. This is possible by a rapid process of self-organization, by which temporal correlations are established and synaptic links are stabilized between corresponding points in image and model, whereas links between noncorresponding points (dashed lines) are temporarily switched off by rapid reversible synaptic plasticity (Wiskott and von der Malsburg, 1995). (This link suppression must only be temporary, as for the next figure presentation a dashed link may be a required one.) In addition to recognition of a figure, dynamic link matching supports also its interpretation, the links forming pointers from abstract model features to the concrete features of the actual figure. Thus, the process supports pattern instantiation.

decoded by object-specific circuits embedded in higher-level cortical areas (presumably IT among them) that are composed of invariant feature cells that are connected among each other in a way that is isomorphic to the arrangement and connectivity of the feature cells in the primary cortices. Thus, any two activated feature cells that are neighbors in primary cortex and correspondingly have an excitatory connection are to be represented by two mutually connected invariant feature cells. Low-level activity can thus be made to resonate with and selectively activate an isomorphic high-level circuit. This principle has been proposed independently (in von der Malsburg, 1981; Hummel and Biederman, 1992) and has been demonstrated to work in computer simulations (von der Malsburg, 1988; Hummel and Biederman, 1992). On this basis, it is possible even to distinguish patterns that contain identical features in different configurations (von der Malsburg and Bienenstock, 1987) (see Figure 3).

Another possibility for reducing feature-correspondence ambiguities relies on more complex feature types, which have a lower probability of occurring multiply in the same input figure. There is little evidence of high-level features in the primary cortices, but the same goal can conveniently be achieved by coarse coding, by coupling the low-level features activated at any point of the sensory surface into one complex feature. This has been realized on the basis of elementary feature types closely corresponding to those actually found in primary visual cortex, formalized as Mallat or Gabor wavelets (Marcelja, 1980; Jones and Palmer, 1987). Such models are highly successful in recognizing arbitrary objects from natural scenes (Konen et al., 1994; von der Malsburg and Reiser, 1995; Wiskott and von der Malsburg, 1995; Würtz, 1997; Kefalea, 1998; Massad et al, 1998). On the basis of these principles, a face recognition system has been built (Okada et al., 1998) that outperformed all competitors in terms of robustness with respect to lighting, pose, and aspect changes in a blind test (Phillips et al., 1998). It is important to note that some of the image variations tested (notably, illumination changes) had not been part of previously delivered training sets and had not been addressed explicitly in the construction of the system, underscoring the generalization power of binding-based systems. Comparison of a simple version of the system (Lades et al., 1993) to human psychophysics of face recognition (Biederman and Kalocsai, 1997) has shown that both the model and human performance scale the same way with task difficulty (i.e., change in pose or expression).

All systems cited in the last two paragraphs make use of a process called "dynamic link matching," that is, they rely on reorganization of the connections between primary and secondary cortices to get rid of ambiguous connections. A problem with this scheme, when based on temporal binding, is the time needed for this reorganization: it usually takes hundreds of iterations to completely decouple noncorresponding regions. Assuming a temporal resolution of a few milliseconds, this translates into several seconds for the recognition of an object, much too long in comparison with observed recognition times, which can be as short as a few dozen milliseconds in the adult (Potter and Levy, 1969). It has been shown, however, that even without any reduction of feature correspondence ambiguities, respectable recognition rates can be achieved if the deformation between training and test figures is not too great (Wiskott, 1999). If a time-economic mechanism for the binding involved in coarse coding of local features could be identified, rapid recognition rates could thus be accounted for.

There is evidence that sensory input can be segmented on the basis of recognized form. This could be implemented by projecting the couplings implicit in high-level form recognition circuits back to the primary cortices. It is true that anatomical studies indicate that back projections from high-order areas such as IT to primary visual cortex are too imprecise for this purpose. However, if dynamic link matching can disambiguate feed-forward connections, it is conceivable that the same disambiguation may also occur for back projections, as is indeed implicit in Wiskott and von der Malsburg (1995). After such disambiguation, the back projections from form recognition circuits on higher levels can then produce precise couplings between points within a figure at a low level.

Whatever the mechanism for recognition, many tasks require the system to establish correspondences between parts of a stored model and the image. A recognition mechanism that relies exclusively on the identification of a summary list of invariant features cannot serve as a basis for this important type of operation.

Instantiation

Pattern instantiation is a very fundamental capability for any intelligent system. It is the mechanism by which new sensory input is interpreted by relating it to known patterns. Patterns may be innate and may be known from previous examples or even from the same sensory input to which they are applied. Pattern instantiation promises to be a very potent basis for learning. If an animal comes genetically equipped with the representation of an abstract schema that describes a class of patterns that is biologically important for it, it can identify instances in its environment and extract and store them selectively. Even without preexisting schemas, very efficient learning is made possible if the organism can find and extract repeating patterns in the environment (Konen and von der Malsburg, 1993).

Pattern instantiation requires that an abstract pattern, composed of certain elements ("roles") and relations, be applied to some sample material by identifying concrete fillers for all the roles in the pattern while preserving their relations. For instantiation to work, bindings between roles and fillers must be kept track of to ensure that there is a one-to-one correspondence between roles and role fillers. Many of the proposed neural mechanisms of pattern recognition content themselves with checking whether all the features expected to be present in the pattern are indeed present in the input, but such mechanisms can neither account for multiple fillers for the same role nor exclude that a single feature erroneously fills several roles, nor is there a provision for checking whether relations that are specified in the abstract pattern are actually satisfied in the instance. Only on the basis of explicit handling of binding relations can these problems be solved.

The examples discussed above amply illustrate the importance and usefulness of a binding mechanism for the brain. Whereas conventional, nonbinding neural network models are mostly still confined to solutions of toy problems and fail when it comes to natural perceptual input, binding-based models for perceptual segmentation and invariant object recognition outdo or at least compare favorably with the best available nonbinding systems. Thus, the conceptual framework of temporal binding has been worked out well enough to serve as a solid basis for neural modeling that goes well beyond the achievements of classical neural networks, at least in the directions probed so far. The examples moreover illustrate that some functional problems of the brain are binding problems, which can only be awkwardly circumvented by classical neural networks.

Conclusion

Although there is a widespread and more or less explicit conviction that classical neural networks are universal (in the sense, "give me a concrete problem and I will devise a network that solves it"), there is no basis for this claim whatsoever. But even if there were, universality cannot solve the brain's problem, which is rather characterized by, "given the concrete network that an individual is born with, learn to cope with situations and problems as they arise" The difference between these two statements is, *first the problem, then the network* (the principle of universality) versus *first the network, then the problem* (the requirement of flexibility)—a very big difference indeed. Any concrete classical neural network, even with arbitrary collections of combination-coding cells, cannot avoid running into binding ambiguities when faced with unexpected problems. Thus, the issue remains to identify in the brain a neural architecture that has the capacity for learning and self-organization and is a fertile basis for all the flexibility and creativity observed in humans and animals. As long as such fundamental problems as instantiation and learning from natural environments remain unsolved (to name but two), there is little reason for anyone to be complacent about the achievements of classical neural networks.

References

A comprehensive reference list for all reviews can be found on pages 111–125.

Neuron, Vol. 24, 111–125, September, 1999, Copyright ©1999 by Cell Press

References for Reviews on the Binding Problem

Abeles, M. (1982a). Role of cortical neuron: integrator or coincidence detector? Israel J. Med. Sci. *18*, 83–92.

Abeles, M. (1982b). Studies of Brain Function, Volume 6, Local Cortical Circuits: An Electrophysiological Study (Berlin: Springer-Verlag).

Abeles, M. (1991). Corticonics: Neural Circuits of Cerebral Cortex (Cambridge: Cambridge University Press).

Abeles, M., Prut, Y., Bergman, H., and Vaadia, E. (1994). Synchronization in neuronal transmission and its importance for information processing. Prog. Brain Res. *102*, 395–404.

Adam, H. (1998). Figur-Grund-Abtrennung mit rückgekoppelten Merkmalsfeldern. PhD Thesis, Department of Physics and Astronomy, Ruhr University, Bochum, Germany.

Adelson, E.H. (1993). Perceptual organization and the judgment of brightness. Science *262*, 2042–2044.

Adelson, E.H. (1999). Lightness perception and lightness illusions. In The Cognitive Neurosciences, M.S. Gazzaniga, ed. (Cambridge, MA: MIT Press).

Adelson, E.H., and Movshon, J.A. (1982). Phenomenal coherence of moving visual patterns. Nature *300*, 523–525.

Aertsen, A., Gerstein, G.L., Habib, M.K., and Palm, G. (1989). Dynamics of neuronal firing correlation: modulation of "effective connectivity." J. Neurophysiol. *61*, 900–917.

Aertsen, A., Diesmann, M., and Gewaltig, M.-O. (1996). Propagation of synchronous spiking activity in feedforward neural networks. J. Physiol. (Paris) *90*, 243–247.

Aiple, F., and Krüger, J. (1988). Neuronal synchrony in monkey striate cortex: interocular signal flow and dependency on spike rates. Exp. Brain Res. *72*, 141–149.

Alais, D., Blake, R., and Lee, S.-H. (1998). Visual features that vary together over time group together over space. Nat. Neurosci. *1*, 160–164.

Albright, T.D., and Stoner, G.R. (1995). Visual motion perception. Proc. Natl. Acad. Sci. USA *92*, 2433–2440.

Alonso, J.-M., and Martinez, L.M. (1998). Functional connectivity between simple cells and complex cells in cat striate cortex. Nat. Neurosci. *1*, 395–403.

Alonso, J.-M., Usrey, W.M., and Reid, R.C. (1996). Precisely correlated firing in cells of the lateral geniculate nucleus. Nature *383*, 815–819.

Andersen, R.A. (1995). Encoding of intention and spatial location in the posterior parietal cortex. Cereb. Cortex *5*, 457–469.

Andersen, R.A. (1997). Multimodal integration for the representation of space in the posterior parietal cortex. Philos. Trans. R. Soc. Lond. B Biol. Sci. *352*, 1421–1428.

Anderson, C.H., and Van Essen, D.C. (1987). Shifter circuits: a computational strategy for dynamic aspects of visual processing. Proc. Natl. Acad. Sci. USA *84*, 6297–6301.

Arbib, M. (1964). Brains, Machines and Mathematics (New York: McGraw-Hill).

Arguin, M., Cavanagh, P., and Joanette, Y. (1994). Visual feature integration with an attention deficit. Brain Cogn. *24*, 44–56.

Arieli, A., Sterkin, A., Grinvald, A., and Aertsen, A. (1996). Dynamics of ongoing activity: explanation of the large variability in evoked cortical responses. Science *273*, 1868–1871.

Ashby, F.G., Prinzmental, W., Ivry, R., and Maddox, W.T. (1996). A formal theory of feature binding in object perception. Psychol. Rev. *103*, 165–192.

Assad, J., and Maunsell, J. (1995). Neuronal correlates of inferred motion in primate posterior parietal cortex. Nature *373*, 518–521.

Bair, W. (1999). Spike timing in the mammalian visual system. Curr Opin. Neurobiol., in press.

Bair, W. and Koch, C. (1995). Precision and reliability of neocortical spike trains in the behaving monkey. In The Neurobiology of Computation, B.J. Kluwer, ed. (New York: Academic Publishers).

Bair, W., and Koch, C. (1996). Temporal precision of spike trains in extrastriate cortex of the behaving monkey. Neural Comput. *8*, 44–66.

Bair, W., and O'Keefe, L.P. (1998). The influence of fixational eye movements on the response of neurons in area MT of the macaque. Vis. Neurosci. *15*, 779–786.

Bair, W., Koch, C., Newsome, W., and Britten, K. (1994). Power spectrum analysis of bursting cells in area MT in the behaving monkey. J. Neurosci. *14*, 2870–2892.

Bair, W., Cavanaugh, J.R., and Movshon, J.A. (1997). Reconstructing stimulus velocity from neuronal responses in area MT. In Advances in Neural Information Processing Systems, M.C. Mozer, M.I. Jordan, and T. Petsche, eds. (Cambridge, MA: MIT Press).

Baldi, P., and Meir, R. (1990). Computing with arrays of coupled oscillators: an application to preattentive texture discrimination. Neural Comput. *2*, 458–471.

Ballard, D.H., Hinton, G.E., and Sejnowski, T.J. (1983). Parallel visual computation. Nature *306*, 21–26.

Barbas, H. (1988). Anatomic organization of basoventral and mediodorsal visual recipient prefrontal regions in the rhesus monkey. J. Comp. Neurol. *276*, 313–342.

Barbas, H., and Pandya, D.N. (1989). Architecture and intrinsic connections of the prefrontal cortex in the rhesus monkey. J. Comp. Neurol. *286*, 353–375.

Barlow, H.B. (1972). Single units and cognition: a neurone doctrine for perceptual psychology. Perception *1*, 371–394.

Barlow, H.B. (1981). Critical limiting factors in the design of the eye and visual cortex. Proc. R. Soc. Lond. B Biol. Sci. *212*, 1–34.

Barlow, H.B. (1985). The twelfth Bartlett memorial lecture: the role of single neurons in the psychology of perception. Quart. J. Exp. Psychol. *37*, 121–145.

Bauer, H.-U., and Pawelzik, K. (1993). Alternating oscillatory and stochastic dynamics in a model for a neuronal assembly. Physica *D69*, 380–393.

Baylis, G.C., Rolls, E.T., and Leonard, C.M. (1985). Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. Brain Res., *342*, 91–102.

Baylis, G.C., Rolls, E.T., and Leonard, C.M. (1987). Functional subdivisions of the temporal lobe neocortex. J. Neurosci. *7*, 330–342.

Beck, J. (1966). Perceptual grouping produced by changes in orientation and shape. Science *154*, 538–540.

Beck, J. (1967). Perceptual grouping produced by line figures. Percep. Psychophys. *2*, 491–495.

Behrmann, M., and Tipper, S.P. (1994). Object-based attentional mechanisms: evidence from patients with unilateral neglect. In Attention and Performance, Volume 15, Conscious and Nonconscious Information Processing, C. Umilta and M. Moscovitch, eds. (Cambridge, MA: MIT Press).

Bergen, J.R., and Adelson, E.H. (1988). Early vision and texture perception. Nature *333*, 363–364.

Bergen, J.R., and Julesz, B. (1983). Parallel versus serial processing in rapid pattern discrimination. Nature *303*, 696–698.

Best, J., Reuss, S., and Dinse, H.R.O. (1986). Lamina-specific differences of visual latencies following photic stimulation in the cat striate cortex. Brain Res. *385*, 356–360.

Biederman, I. (1981). On the semantics of a glance at a scene. In Perceptual Organization, M. Kubovy and J. Pomerantz, eds. (Hillsdale, NJ: Lawrence Erlbaum Associates).

Biederman, I. (1987). Recognition by components: A theory of human image understanding. Psychol. Rev. *94*, 115–147.

Biederman, I. and Kalocsai, P. (1997). Neurocomputational bases of object and face recognition. Philos. Trans. R. Soc. Lond. B Biol. Sci. *352*, 1203–1219.

Bienenstock, E. (1995). A model of neocortex. Network *6*, 179–224.

Bienenstock, E., and von der Malsburg, C. (1987). A neural network for invariant pattern recognition. Europhys. Lett. *4*, 121–126.

Blake, R., and Yang, Y. (1997). Spatial and temporal coherence in perceptual binding. Proc. Natl. Acad. Sci. USA *94*, 7115–7119.

Booth, M., and Rolls, E. (1998). View-invariant representations of familiar objects by neurons in the inferior temporal visual cortex. Cereb. Cortex *8*, 510–523.

Borg-Graham, L., Monier, C., and Fregnac, Y. (1996). Voltage-clamp measurement of visually-evoked conductances with whole-cell patch recordings in primary visual cortex. J. Physiol. (Paris) *90*, 185–188.

Borg-Graham, L.J., Monier, C., and Fregnac, Y. (1998). Visual input evokes transient and strong shunting inhibition in visual cortical neurons. Nature *393*, 369–373.

Borisyuk, R.M., Borisyuk, G.N., and Kazanovich, Y.B. (1998). The synchronization principle in modelling of binding and attention. Membr. Cell Biol. *11*, 753–761.

Bosking, W.H, Zhang, Y., Schofield, B., and Fitzpatrick, D. (1997). Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex. J. Neurosci. *17*, 2112–2127.

Boussaoud, D., Ungerleider, L.G., and Desimone, R. (1990). Pathways for motion analysis: cortical connections of the medial superior temporal and fundus of the superior temporal visual area in the macaque. J. Comp. Neurol. *296*, 462–495.

Bouyer, J.J., Montaron, M.F., and Rougeul, A. (1981). Fast fronto-parietal rhythms during combined focused attentive behaviour and immobility in cat: cortical and thalamic localizations. Electroenceph-alogr. Clin. Neurophysiol. *51*, 244–252.

Bradley, D.C., Chang, G.C., and Andersen, R.A. (1998). Encoding of three-dimensional structure-from-motion by primate area MT neurons. Nature *392*, 714–717.

Bragin, A., Jando, G., Nadasdy, Z., Hetke, J., Wise, K., and Buzsaki, G. (1995). Gamma (40–100 Hz) oscillation in the hippocampus of the behaving rat. J. Neurosci. *15*, 47–60.

Braitenberg, V. (1978). Cell assemblies in the cerebral cortex. In Lecture Notes in Biomathematics, Volume 21, Theoretical Approaches in Complex Systems, R. Heim and G. Palm, eds. (Berlin: Springer).

Braitenberg, V., and Schuz, A. (1991). Anatomy of the Cortex: Statistics and Geometry (Berlin: Springer).

Braun, J., and Julesz, B. (1998). Dividing attention at little cost: detection and discrimination tasks. Percept. Psychophys. *60*, 1–23.

Bravo, M., and Blake, R. (1990). Preattentive vision and perceptual groups. Perception *19*, 515–522.

Brecht, M., Singer, W., and Engel, A.K. (1998). Correlation analysis of corticotectal interactions in the cat visual system. J. Neurophysiol. *79*, 2394–2407.

Bressler, S.L., Coppola, R., and Nakamura, R. (1993). Episodic multiregional cortical coherence at multiple frequencies during visual task performance. Nature *366*, 153–156.

Briand, K.A., and Klein, R.M. (1987). Is Posner's "beam" the same as Triesman's "glue"? On the relation between visual orienting and feature integration theory. J. Exp. Psychol. Hum. Percept. Perform. *13*, 228–241.

Britten, K.H., Shadlen, M.N., Newsome, W.T., and Movshon, J.A. (1992). The analysis of visual motion: a comparison of neuronal and psychophysical performance. J. Neurosci. *12*, 4745–4765.

Britten, K.H., Newsome, W.T., Shadlen, M.N., Celebrini, S., and Movshon, J.A. (1996). A relationship between behavioral choice and the visual responses of neurons in macaque MT. Vis. Neurosci. *13*, 87–100.

Brody, C.D. (1998). Slow covariations in neuronal resting potentialscan lead to artefactually fast cross-correlations in their spike trains. J. Neurophysiol. *80*, 3345–3351.

Brody, C.D. (1999a). Disambiguating different covariation types. Neural Comput. *11*, 1527–1535.

Brody, C.D. (1999b). Correlations without synchrony. Neural Comput. *11*, 1537–1551.

Brody, C.D. (1999c). Latency, excitability, and spike timing covariations. Neural Comput., in press.

Bruce, C., Desimone, R., and Gross, C. (1981). Visual properties of neurons in a polysensory area in the superior temporal sulcus of the macaque. J. Neurophysiol. *46*, 369–384.

Bülthoff, H., and Edelman, S. (1992). Psychophysical support for a two-dimensional view interpolation theory of object recognition. Proc. Natl. Acad. Sci. USA *89*, 60–64.

Bülthoff, H.H., Edelman, S.Y., and Tarr, M.J. (1995). How are three-dimensional objects represented in the brain? Cereb. Cortex *3*, 247–260.

Buračas, G., Zador, A., DeWeese, M., and Albright, T. (1998). Efficient discrimination of temporal patterns by motion-sensitive neurons in primate visual cortex. Neuron *20*, 959–969.

Burr, D. (1979). Acuity for apparent vernier offset. Vision Res. *19*, 835–837.

Bush, P., and Sejnowski, T. (1996). Inhibition synchronizes sparsely connected cortical neurons within and between columns in realistic network models. J. Comput. Neurosci. *3*, 91–110.

Bushnell, M.C., Goldberg, M.E., and Robinson, D.L. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. J. Neurophysiol. *46*, 755–772.

Buzsaki, G. (1996). The hippocampo-neocortical dialogue. Cereb. Cortex *6*, 81–92.

Buzsaki, G., and Chrobak, J.J. (1995). Temporal structure in spatially organized neuronal ensembles: a role for interneuronal networks. Curr. Opin. Neurobiol. *5*, 504–510.

Buzsaki, G., Leung, L.S., and Vanderwolf, C.H. (1983). Cellular basis of hippocampal EEG in the behaving rat. Brain Res. *6*, 139–171.

Caminiti, R., Ferraina, S., and Johnson, P.B. (1996). The sources of visual information to the primate frontal lobe: a novel role for the superior parietal lobule. Cereb. Cortex *6*, 319–328.

Carney, T., Paradiso, M., and Freeman, R. (1989). A physiological correlate of the Pulfrich effect in cortical neurons of the cat. Vision Res. *29*, 155–165.

Carney, T., Silverstein, D., and Klein, S. (1995). Vernier acuity during image rotation and translation: visual performance limits. Vision Res. *35*, 1951–1964.

Castelo-Branco, M., Neuenschwander, S., and Singer, W. (1998). Synchronization of visual responses between the cortex, lateral geniculate nucleus, and retina in the anesthetized cat. J. Neurosci. *18*, 6395–6410.

Cave, K.R. (1999). The Feature Gate model of visual selection. Psychol. Res., in press.

Cave, K.R., and Bichot, N.P. (1999). Visuo-spatial attention: beyond a spotlight model. Psychonom. Bull. Rev., in press.

Cave, K.R., and Kosslyn, S.M. (1989). Varieties of size-specific visual selection. J. Exp. Psychol. Gen. *118*, 148–164.

Cave, K.R., and Wolfe, J.M. (1990). Modeling the role of parallel processing in visual search. Cogn. Psychol. *22*, 225–271.

Chance, F., Nelson, S., and Abbott, L. (1999). Complex cells as cortically amplified simple cells. Nat. Neurosci. *2*, 277–282.

Chelazzi, L., Miller, E.K., Duncan, J., and Desimone, R.C. (1993). A neural basis for visual search in inferior temporal cortex. Nature *363*, 345–347.

Chelazzi, L., Duncan, J., Miller, E.K., and Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. J. Neurophysiol. *80*, 2918–2940.

Cheng, K., Hasegawa, T., Saleem, K.S., and Tanaka, K. (1994). Comparison of neuronal selectivity for stimulus speed, length, and contrast in the prestriate visual cortex areas V4 and MT of the macaque monkey. J. Neurophysiol. *71*, 2269–2280.

Chino, Y., Shansky, M., Jankowski, W., and Banser, F. (1983). Effects of rearing kittens with convergent strabismus on development of receptive-field properties in striate cortex neurons. J Neurophysiol. *50*, 265–286.

Chino, Y.M., Smith, E.L., Wada, H., Ridder, W.H., Langston, A.L., and Lesher, G.A. (1991). Disruption of binocularly correlated signals alters the postnatal development of spatial properties in cat striate cortical neurons. J. Neurophysiol. *65*, 841–859.

Chrobak, J.J., and Buzsaki, G. (1998). Gamma oscillations in the entorhinal cortex of the freely behaving rat. J. Neurosci. *18*, 388–398.

Churchland, P.S., Ramachandran, V.S., and Sejnowski, T.J. (1994). A critique of pure vision. In Large-Scale Neuronal Theories of the Brain, C. Koch and J.L. Davis, eds. (Cambridge, MA: MIT Press).

Cobb, S.R., Buhl, E.H., Halasy, K., Paulsen, O., and Somogyi, P. (1995). Synchronization of neuronal activity in hippocampus by individual GABAergic interneurons. Nature *378*, 75–78.

Cohen, A., and Ivry, R.B. (1989). Illusory conjunctions inside and outside the focus of attention. J. Exp. Psychol. Hum. Percept. Perform. *15*, 650–663.

Cohen, A., and Ivry, R.B. (1991). Density effects in conjunction search: evidence for coarse location mechanism of feature integration. J. Exp. Psychol. Hum. Percept. Perform. *17*, 891–901.

Colby, C.L., and Goldberg, M.E. (1999). Space and attention in parietal cortex. Annu. Rev. Neurosci. *22*, 319–349.

Colby, C.L., Duhamel, J.-R., and Goldberg, M.E. (1996). Visual, presaccadic, and cognitive activation of single neurons in monkey lateral intraparietal area. J. Neurophysiol. *76*, 2841–2852.

Connor, C.E., Gallant, J.L., Preddie, D.C., and Van Essen, D.C. (1996). Responses in area V4 depend on the spatial relationship between stimulus and attention. J. Neurophysiol. *75*, 1306–1308.

Connor, C., Preddie, D., Gallant, J., and van Essen, D. (1997). Spatial attention effects in macaque area V4. J. Neurosci. *17*, 3201–3214.

Connors, B.W., and Gutnick, M.J. (1990). Intrinsic firing patterns of diverse neocortical neurons. Trends Neurosci. *13*, 99–104.

Connors, B.W., Gutnick, M.J., and Prince, D.A. (1982). Electrophysiological properties of neocortical neurons in vitro. J. Neurophysiol. *48*, 1302–1320.

Corbetta, M., Miezin, F.M., Shulman, G.L., and Petersen, S.E. (1993). A PET study of visuospatial attention. J. Neurosci. *13*, 1202–1226.

Corbetta, M., Shulman, G.L., Miezin, F.M., and Petersen, S.E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. Science *270*, 802–805.

Cowey, A., and Gross, C.G. (1970). Effects of foveal prestriate and inferotemporal lesions on visual discrimination by rhesus monkeys. Exp. Brain Res. *11*, 128–144.

Creutzfeldt, O.D., Garey, L.J., Kuroda, R., and Wolff, J.R. (1977). The distribution of degenerating axons after small lesions in the intact and isolated visual cortex of the cat. Exp. Brain Res. *27*, 419–440.

Crewther, D., and Crewther, S. (1990). Neural site of strabismic amblyopia in cats: spatial frequency deficit in primary cortical neurons. Exp. Brain Res. *79*, 615–622.

Crick, F. (1984). Function of the thalamic reticular complex: the searchlight hypothesis. Proc. Natl. Acad. Sci. USA *81*, 4586–4590.

Crick, F., and Koch, C. (1990a). Some reflections on visual awareness. Cold Spring Harbor Symp. Quant. Biol. *55*, 953–962.

Crick, F., and Koch, C. (1990b). Towards a neurobiological theory of consciousness. Sem. Neurosci. *2*, 263–275.

Damasio, A.R. (1985). Disorders of complex visual processing: agnosia, achromatopsia, Balint's syndrome, and related difficulties of orientation and construction. In Principles of Behavioral Neurology, M.M. Mesulam, ed. (Philadelphia: Davis).

Das, A., and Gilbert, C.D. (1995). Receptive field expansion in adult visual cortex is linked to dynamic changes in strength of cortical connections. J. Neurophysiol. *74*, 779–792.

Das, A., and Gilbert, C.D. (1999). Topography of contextual modulations mediated by short-range interactions in primary visual cortex. Nature *399*, 655–661.

Dean, P. (1976). Effects of inferotemporal lesions on the behavior of monkeys. Psychol. Bull. *83*, 41–71.

DeAngelis, G.C., Ghose, G.M., Ohzawa, I., and Freeman, R.D. (1999). Functional micro-organization of primary visual cortex: receptive field analysis of nearby neurons. J. Neurosci. *19*, 4046–4064.

deCharms, R., and Merzenich, M. (1996). Primary cortical representation of sounds by the coordination of action-potential timing. Nature *381*, 610–613.

DeCharms, R.C., Blake, D.T., and Merzenich, M.M. (1998). Optimizing sound features for cortical neurons. Science *280*, 1439–1443.

De Oliveira, S.C., Thiele, A., and Hoffmann, K.P. (1997). Synchronization of neuronal activity during stimulus expectation in a direction discrimination task. J. Neurosci. *17*, 9248–9260.

Deppisch, J., Bauer, H.-U., Schillen, T.B., König, P., Pawelzik, K., and Geisel, T. (1993). Alternating oscillatory and stochastic states in a network of spiking neurons. Network *4*, 243–257.

Desimone, R. (1991). Face-selective cells in the temporal cortex of monkeys. J. Cogn. Neurosci. *3*, 1–8.

Desimone, R., and Duncan, J. (1995). Neural mechanisms of selective visual attention. Annu. Rev. Neurosci. *18*, 193–222.

Desimone, R., and Schein, S. (1987). Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. J. Neurophysiol. *57*, 835–868.

Desimone, R., and Ungerleider, L. (1986). Multiple visual areas in the caudal superior temporal sulcus of the macaque. J. Comp. Neurol. *248*, 164–189.

Desimone, R., Albright, T.D., Gross, C.G., and Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. J. Neurosci. *4*, 2051–2062.

Desimone, R., Schein, S.J., Moran, J., and Ungerleider, L.G. (1985). Contour, color and shape analysis beyond the striate cortex. Vision Res. *25*, 441–452.

Dev, P. (1975). Perception of depth surfaces in random-dot stereograms: a neural model. Int. J. Man-Machine Stud. 7, 511–528.

DeValois, R.L., and DeValois, K.K. (1988). Spatial Vision (New York: Oxford University Press).

DeValois, R.L., Albrecht, D.G., and Thorell, L.G. (1982a). Spatial frequency selectivity of cells in macaque visual cortex. Vision Res. *22*, 545–559.

DeValois, R.L., Yund, E.W., and Hepler, N. (1982b). The orientation and direction selectivity of cells in macaque visual cortex. Vision Res. *22*, 531–544.

DeYoe, E.A., and Van Essen, D.C. (1985). Segregation of efferent connections and receptive field properties in visual area V2 of the macaque. Nature *317*, 58–61.

DeYoe, E.A., and Van Essen, D.C. (1988). Concurrent processing streams in monkey visual cortex. Trends Neurosci. *11*, 219–226.

Diesmann, M., Gewaltig, M.-O., and Aertsen, A. (1997). Cortical synfire activity—a two dimensional state space analysis. In From Membrane to Mind: Proceedings of the 25th Gottinger Neurobiology Conference, H. Wassle and N. Elsner, eds. (Stuttgart: Thieme-Verlag).

Dixon, P., and Shedden, J.M. (1987). Conceptual and physical differences in the category effect. Percept. Psychophys. *42*, 457–464.

Dodwell, P.C., and Humphrey, G.K. (1992). A functional theory of the McCollough effect. Psych. Rev. *97*, 78–89.

Donnelly, N., Humphreys, G.W., and Riddoch, M.J. (1991). Parallel computation of primitive shape descriptions. J. Exp. Psychol. Hum. Percep. Perform. *17*, 561–570.

Donoghue, J.P., Sanes, J.N., Hatsopoulos, N.G., and Gaal, G. (1998). Neural discharge and local field potential oscillations in primate motor cortex during voluntary movement. J. Neurophysiol. *79*, 159–173.

Doupe, A.J. (1997). Song- and order-selective neurons in the songbird anterior forebrain and their emergence during vocal development. J. Neurosci. *17*, 1147–1167.

Dubner, R., and Zeki, S.M. (1971). Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus. Brain Res. *35*, 528–532.

Duncan, J. (1983). Category effects in visual search: a failure to replicate the "oh-zero" phenomenon. Percept. Psychophys. *34*, 221–232.

Duncan, J. (1984). Selective attention and the organization of visual information. J. Exp. Psychol. Gen. *113*, 501–517.

Eckes, C., and Vorbrüggen, C.V. (1996). Combining data-driven and model-based cues for segmentation of video sequences. In WCNN 1996 (San Diego: Lawrence Erlbaum).

Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., and Reitboeck, H.J. (1988). Coherent oscillations: a mechanism for feature linking in the visual cortex? Biol. Cybern. *60*, 121–130.

Eckhorn, R., Frien, A., Bauer, R., Woelbern, T., and Kehr, H. (1993). High frequency 60–90 Hz oscillations in primary visual cortex of awake monkey. Neuroreport *4*, 243–246.

Edelman, G.M. (1978). Group selection and phasic reentrant signaling: a theory of higher brain function. In The Mindful Brain: Cortical Organization and the Group-Selective Theory of Higher Brain Function. G.M. Edelman and V.B. Mountcastle, eds. (Cambridge, MA: MIT Press).

Edelman, G.M. (1987). Neural Darwinism: The Theory of Neuronal Group Selection (New York: Basic Books).

Edelman, G.M. (1989). The Remembered Present: A Biologoical Theory of Consciousness (New York: Basic Books).

Edwards, D.P., Purpura, K.P., and Kaplan, E. (1995). Contrast sensitivity and spatial frequency response of primate cortical neurons in and around the cytochrome oxidase blobs. Vision Res. *35*, 1501–1523.

Eggers, H., and Blakemore, C. (1978). Physiological basis of an isometropic amblyopia. Science *201*, 264–267.

Elder, J., and Zucker, S. (1993). The effect of contour closure on the rapid discrimination of two-dimensional shapes. Vision Res. *33*, 981–991.

Engel, A.K., König, P., Gray, C.M., and Singer, W. (1990). Stimulus-dependent neuronal oscillations in cat visual cortex: inter-columnar interaction as determined by cross-correlation analysis. Eur. J. Neurosci. *2*, 588–606.

Engel, A.K., König, P., Kreiter, A.K., and Singer, W. (1991a). Interhemispheric synchronization of oscillatory neuronal responses in cat visual cortex. Science *252*, 1177–1179.

Engel, A.K., Kreiter, A.K., König, P., and Singer, W. (1991b). Synchronization of oscillatory neuronal responses between striate and extrastriate visual cortical areas of the cat. Proc. Natl. Acad. Sci. USA *88*, 6048–6052.

Engel, A.K., König, P., and Singer, W. (1991c). Direct physiological evidence for scene segmentation by temporal coding. Proc. Natl. Acad. Sci. USA *88*, 9136–9140.

Engel, A.K., König, P., and Singer, W. (1992a). Reply to: The functional nature of neuronal oscillations. Trends Neurosci. *15*, 387–388.

Engel, A.K., König, P., Kreiter, A.K., Chillen, T.B., and Singer, W. (1992b). Temporal coding in the visual cortex: new vista on integration in the nervous system. Trends Neurosci. *15*, 218–225.

Engel, A.K., Roelfsema, P.R., Fries, P., Brecht, M., and Singer, W. (1997). Role of the temporal domain for response selection and perceptual binding. Cereb. Cortex *7*, 571–582.

Eskandar, E.N., and Assad, J.A. (1999). Dissociation of visual motor and predictive signals in parietal cortex during visual guidance. Nat. Neurosci. *2*, 88–93.

Fahle, M., and Koch, C. (1995). Spatial displacement, but not temporal asynchrony, destroys figural binding. Vision Res. *35*, 491–494.

Fahle, M., and Poggio, T. (1981). Visual hyperacuity: spatio-temporal interpolation in human vision. Proc. R. Soc. Lond. B Biol. Sci. *213*, 451–477.

Fang, S.-P., and Wu, P. (1989). Illusory conjunctions in the perception of Chinese characters. J. Exp. Psychol Hum. Percept. Perform. *15*, 434–447.

Felleman, D.J., and Van Essen, D.C. (1987). Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex. J. Neurophysiol. *57*, 889–920.

Felleman, D.J., and van Essen, D.C. (1991). Distributed hierarchical processing in the primate cerebral cortex. Cereb. Cortex *1*, 1–47.

Ferrera, V.P., and Lisberger, S.G. (1995). Attention and target selection for smooth pursuit eye movements. J. Neurosci. *15*, 7472–7484.

Ferrera, V.P., Rudolph, K.K., and Maunsell, J.H.R. (1994). Responses of neurons in the parietal and temporal visual pathways during a motion task. J. Neurosci. *14*, 6171–6186.

Fetz, E., Toyama, K., and Smith, W. (1991). Synaptic interactions between cortical neurons. In Cerebral Cortex, A. Peters and E.G. Jones, eds. (New York: Plenum Press).

Fodor, J.A., and Pylyshyn, Z.W. (1988). Connectionism and cognitive architecture: a critical analysis. Cognition *28*, 3–71.

Folk, C.L., and Egeth, H. (1989). Does the identification of simple features require serial processing? J. Exp. Psychol. Hum. Percept. Perform. *15*, 97–110.

Foster, K.H., Gaska, J.P., Nagler, M., and Pollen, D.A. (1985). Spatial and temporal frequency selectivity of neurones in visual cortical areas V1 and V2 of the macaque monkey. J. Physiol. (Lond.) *365*, 331–363.

Franz, V., Gegenfurtner, K.R., Fahle, M., and Buelthoff, H.H. (1999). Grasping visual illusions: no evidence for a dissociation between perception and action. Psychol. Sci., in press.

Freeman, W.J. (1975). Mass Action in the Nervous System (NewYork: Academic Press).

Freeman, W.J., and Skarda, C.A. (1985). Spatial EEG-patterns, nonlinear dynamics and perception: the neo-Sherrington view. Brain Res. Rev. *10*, 147–175.

Freiwald, W.A., Kreiter, A.K., and Singer, W. (1995). Stimulus dependent intercolumnar synchronization of single unit responses in cat area 17. Neuroreport *6*, 2348–2352.

Friedman-Hill, S.R., Robertson, L.C., and Treisman, A. (1995). Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions. Science *269*, 853–855.

Friedman-Hill, S., Maldonado, P.E., and Gray, C.M. (1999). Temporal dynamics of neuronal activity in the striate cortex of alert macaque: I. Incidence and stimulus-dependence of oscillations. J. Neurosci., in press.

Frien, A., Eckhorn, R., Bauer, R., Woelbern, T., and Kehr, H. (1994). Stimulus-specific fast oscillations at zero phase between visual areas V1 and V2 of awake monkey. Neuroreport *5*, 2273–2277.

Fries, P., Roelfsema, P.R., Engel, A.K., König, P., and Singer, W. (1997). Synchronization of oscillatory responses in visual cortex correlates with perception in interocular rivalry. Proc. Natl. Acad. Sci. USA *94*, 12699–12704.

Fuji, H., Ito, H., Aihara, K., Ichinose, N., and Tsukada, M. (1996). Dynamical cell assembly hypothesis-theoretical possibility of spatio-temporal coding in the cortex. Neural Network *9*, 1303–1350.

Fujita, I., Tanaka, K., Ito, M., and Cheng, K. (1992). Columns for visual features of objects in monkey inferotemporal cortex. Nature *360*, 343–346.

Fukushima, K. (1980). Neocognitron: a self-organizing neural network model for a mechanism of pattern recognition unaffected by shift in position. Biol. Cybern. *36*, 193–202.

Gallant, J.L., Connor, C.E., Rakshit, S., Lewis, J.W., and Van Essen, D.C. (1996). Neural responses to polar, hyperbolic, and cartesian gratings in area V4 of the macaque monkey. J. Neurophysiol. *76*, 2718–2739.

Gattass, R., Sousa, A.P., and Gross, C.G. (1988). Visuotopic organization and extent of V3 and V4 of the macaque. J. Neurosci. *8*, 1831–1845.

Gawne, T.J., Kjaer, T.W., and Richmond, B.J. (1996). Latency: another potential code for feature binding in striate cortex. J. Neurophysiol. *76*, 1356–1360.

Geesaman, B.J., and Andersen, R.A. (1996). The analysis of complex motion patterns by form/cue invariant MSTd neurons. J. Neurosci. *16*, 4716–4732.

Geisler, W.S., and Albrecht, D.G. (1995). Bayesian analysis of identification performance in monkey visual cortex: nonlinear mechanisms and stimulus certainty. Vision Res. *35*, 2723–2730.

Georgopoulos, A.P., Ashe, J., Smyrnis, N., and Taira, M. (1992). The motor cortex and the coding of force. Science *256*, 1692–1695.

Gerstein, G.L., Bedenbaugh, P., and Aertsen, M.H. (1989). Neuronal assemblies. IEEE Trans. Biomed. Eng. *36*, 4–14.

Gerstner, W., and van Hemmen, J.L. (1993). Coherence and incoherence in a globally coupled ensemble of pulse-emitting units. Phys. Rev. Lett. *7*, 312–315.

Gerstner, W., Kempter, R., Van Hemmen, J.L., and Wagner, H. (1996). A neuronal learning rule for sub-millisecond temporal coding. Nature *383*, 76–78.

Ghose, G.M., and Freeman, R.D. (1992). Oscillatory discharge in the visual system: does it have a functional role? J. Neurophysiol. *68*, 1558–1574.

Ghose, G.M., and Freeman, R.D. (1997). Intracortical connections are not required for oscillatory activity in the visual cortex. Vis. Neurosci. *14*, 963R–979R.

Ghose, G.M., and Maunsell, J. (1999). Specialized representations in visual cortex: a role for binding? Neuron *24*, this issue, 79–85.

Ghose, G.M., and Ts'o, D.Y. (1997). Form processing modules in primate area V4. J. Neurophysiol. *77*, 2191–2196.

Gibson, J.R., and Maunsell, J.H.R. (1997). The sensory modality specificity of neural activity related to memory in visual cortex. J. Neurophysiol. *78*, 1263–1275.

Gilbert, C.D., and Wiesel, T.N. (1979). Morphology and intracortical projections of functionally characterised neurones in the cat visual cortex. Nature *280*, 120–125.

Gilbert, C.D., and Wiesel, T.N. (1983). Clustered intrinsic connections in cat visual cortex. J. Neurosci. *3*, 1116–1133.

Gilbert, C.D., and Wiesel, T.N. (1989). Columnar specificity of intrinsic horizontal and cortico-cortical connections in cat visual cortex. J. Neurosci. *9*, 2432–2442.

Givre, S.J., Arezzo, J.C., and Schroeder, C.E. (1995). Effects of wavelength on the timing and laminar distribution of illuminance-evoked activity in macaque V1. Vis. Neurosci. *12*, 229–239.

Gizzi, M.S., Newsome, W.T., and Movshon, J.A. (1983). Directional selectivity of neurons in macaque MT. Invest. Ophthal. Vis. Sci. *24 (suppl.)*, 107.

Gizzi, M.S., Katz, E., Schumer, R.A., and Movshon, J.A. (1990). Selectivity for orientation and direction of motion of single neurons in cat striate and extrastriate visual cortex. J. Neurophysiol. *63*, 1529–1543.

Goldsmith, M. (1998). What's in a location? Comparing object-based and space-based models of feature integration in visual search. J. Exp. Psychol. *127*, 189–219.

Goldstone, R.L. (1998). Perceptual learning. Annu. Rev. Psychol. *49*, 585–612.

Goodale, M. (1993). Visual pathways supporting perception and action in the primate cerebral cortex. Curr. Opin. Neurobiol. *3*, 578–585.

Goodale, M., and Humphrey, G. (1998). The objects of action and perception. Cognition *67*, 181–207.

Goodale, M.A., and Milner, A.D. (1992). Separate visual pathways for perception and action. Trends Neurosci. *15*, 20–25.

Goodale, M.A., Milner, A.D., Jakobson, L.S., and Carey, D.P. (1991). A neurological dissociation between perceiving objects and grasping them. Nature *349*, 154–156.

Goodale, M.A., Meenan, J.P., Bulthoff, H.H., Nicolle, D.A., Murphy, K. J., and Racicot, C.I. (1994). Separate neural pathways for visual analysis of object shape in perception and prehension. Curr. Biol. *4*, 604–610.

Goolkasian, P. (1988). Illusory conjunctions in the processing of clock times. J. Gen. Psychol. *115*, 341–353.

Gottlieb, J.P., Kusunoki, M., and Goldberg, M.E. (1998). The representation of visual salience in monkey parietal cortex. Nature *391*, 481–484.

Graham, N. (1989). Visual Pattern Analyzers (New York: Oxford University Press).

Gray, C.M. (1994). Synchronous oscillations in neuronal systems: mechanisms and functions. J. Comput. Neurosci. *1*, 11–38.

Gray, C.M. (1999). The temporal correlation hypothesis of visual feature integration: still alive and well. Neuron *24*, this issue, 31–47.

Gray, C.M., and McCormick, D.A. (1996). Chattering cells: superficial pyramidal neurons contributing to the generation of synchronous oscillations in the visual cortex. Science *274*, 109–113.

Gray, C.M., and Singer, W. (1989). Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. Proc. Natl. Acad. Sci. USA *86*, 1698–1702.

Gray, C.M., and Viana Di Prisco, G. (1997). Stimulus-dependent neuronal oscillations and local synchronization in striate cortex of the alert cat. J. Neurosci. *17*, 3239–3253.

Gray, C.M., Koenig, P., Engel, A.K., and Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. Nature *338*, 334–337.

Gray, C.M, Engel, A.K., Koenig, P., and Singer, W. (1990). Stimulus-dependent neuronal oscillations in cat visual cortex: receptive field properties and feature dependence. Eur. J. Neurosci. *2*, 607–619.

Gray, C.M., Engel, A.K., Koenig, P., and Singer, W. (1992). Synchronization of oscillatory neuronal responses in cat striate cortex: temporal properties. Vis. Neurosci. *8*, 337–347.

Green, M. (1992). Visual search: detection, identification and localization. Perception *21*, 765–777.

Gregory, R.L. (1970). The Intelligent Eye (London: Weidenfield and Nicholson).

Gross, C.G., Cowey, A., and Manning, F.J. (1971). Further analysis of visual discrimination deficits following foveal prestriate and inferotemporal lesions in rhesus monkeys. J. Comp. Physiol. Psychol. *76*, 1–7.

Gross, C.G., Rocha-Miranda, C.E., and Bender, D.B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. J. Neurophysiol. *35*, 96–111.

Grossberg, S. (1995). The attentive brain. Am. Scientist *83*, 438–449.

Grossberg, S. (1999a). The link between brain learning, attention, and consciousness. Conscious. Cogn., in press.

Grossberg, S. (1999b). How does the cerebral cortex work? Spat. Vis., in press.

Grossberg, S., and Somers, D. (1991). Synchronized oscillations during cooperative feature linking in a cortical model of visual perception. Neural Networks *4*, 453–466.

Haenny, P.D., Maunsell, J.H.R., and Schiller, P.H. (1988). State dependent activity in monkey visual cortex. II. Retinal and extraretinal factors in V4. Exp. Brain Res. *69*, 245–259.

Hata, Y., Tsumoto, T., Sato, H., and Tamura, H. (1991). Horizontal interactions between visual cortical neurones studied by cross-correlation analysis in the cat. J. Physiol. *441*, 593–614.

Hatsopoulos, N.G., Ojakangas, C.L., Paninski, L., and Donoghue, J.P. (1998). Information about movement direction obtained from synchronous activity of motor cortical neurons. Proc. Natl. Acad. Sci. USA *95*, 15706–15711.

Hayek, F.A. (1952). The Sensory Order (Chicago: University of Chicago Press).

Hebb, D.O. (1949). The Organization of Behavior (New York: Wiley).

Heeger, D. (1992). Normalization of cell responses in cat striate cortex. Vis. Neurosci. *9*, 181–197.

Hellwig, B., Schuz, A., and Aertsen, A. (1994). Synapses on axon collaterals of pyramidal cells are spaced at random intervals: a Golgi study in the mouse cerebral cortex. Biol. Cybern. *71*, 1–12.

Herculano-Houzel, S., Munk, M.H., Neuenschwander, S., and Singer, W. (1999). Precisely synchronized oscillatory firing patterns require electroencephalographic activation. J. Neurosci. *19*, 3992–4010.

Hess, R., Campbell, F., and Greenhalgh, T. (1978). On the nature of the neural abnormality in human amblyopia: neural aberrations and neural sensitivity loss. Pflügers Arch. *377*, 201–207.

Hinton, G.E.A. (1981). A parallel computation that assigns canonical object-based frames of reference. In Proceedings of the Seventh International Joint Conference on Artificial Intelligence, Volume 2 (Vancouver).

Hoffman, J.E. (1979). A two-stage model of visual search. Percept. Psychophys. *25*, 319–327.

Hoffman, D.A., Magee, J.C., Colbert, C.M., and Johnston, D. (1997). K+ channel regulation of signal propagation in dendrites of hippocampal pyramidal neurons. Nature *387*, 869–875.

Hommel, B. (1998). Event files: evidence for automatic integration of stimulus-response episodes. Vis. Cogn. *5*, 183–216.

Hopfield, J.J., and Hertz, A.V.M. (1995). Rapid local synchronization of action potentials: toward computation with coupled integrate-and-fire neurons. Proc. Natl. Acad. Sci. USA *92*, 6655–6662.

Hoppensteadt, F.C., and Izhikevich, E.M. (1998). Thalamo-cortical interactions modeled by weakly connected oscillators: could the brain use FM radio principles? Biosystems *48*, 85–94.

Horwitz, G.D., and Newsome, W.T. (1999). Separate signals for target selection and movement specification in the superior colliculus. Science *284*, 1158–1161.

Houck, M.R., and Hoffman, J.E. (1986). Conjunction of color and form without attention. Evidence from an orientation-contingent color aftereffect. J. Exp. Psychol. Hum. Percept. Perform. *12*, 186–199.

Howard, I.P., and Rogers, B.J. (1995). Binocular Vision and Stereopsis (Oxford: Oxford University Press).

Hubel, D., and Wiesel, T. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J. Physiol. *160*, 106–154.

Hubel, D., and Wiesel, T. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. J. Neurophysiol. *28*, 229–289.

Hubel, D.H., and Wiesel, T.N. (1968). Receptive fields and functional architecture of monkey striate cortex. J. Physiol. (Lond.) *195*, 215–243.

Hubel, D.H., and Wiesel, T.N. (1974). Sequence regularity and geometry or orientation columns in the monkey striate cortex. J. Comp. Neurol. *158*, 267–294.

Huerta, P.T., and Lisman, J.E. (1996). Low-frequency stimulation at the throughs of Q-oscillation induces long-term depression of previously potentiated CA1 synapses. J. Neurophysiol. *75*, 877–884.

Hummel, J.E., and Biederman, I. (1992). Dynamic binding in a neural network for shape recognition. Psychol. Rev. *99*, 480–517.

Hummel, J.E., and Stankiewicz, B.J. (1996). An architecture for rapid, hierarchical structural description. In Attention and Performance, Volume XVI, T. Inui and J. McClelland, eds. (Cambridge, MA: MIT Press).

Intraub, H. (1981). Identification and naming of briefly glimpsed visual scenes. In Eye Movement: Cognition and Visual Perception, D.F. Fisher, R.A. Monty, and J.W. Senders, eds. (Hillsdale, NJ: Lawrence Erlbaum Associates).

Intraub, H. (1985). Visual dissociation: an illusory conjunction of pictures and forms. J. Exp. Psychol. Hum. Percept. Perform. *11*, 431–442.

Ito, M., and Gilbert, C.D. (1999). Attention modulates contextual influences in the primary visual cortex of alert monkeys. Neuron *22*, 593–604.

Ivry, R.B., and Prinzmetal, W. (1991). Effect of feature similarity on illusory conjunctions. Percept. Psychophys. *49*, 105–116.

Jensen, O., and Lisman, J.E. (1998). An oscillatory short-term memory buffer model can account for data on the Sternberg task. J. Neurosci. *18*, 10688–10699.

Johnston, D., Magee, J.C., Colbert, C.M., and Christie, B.R. (1996). Active properties of neuronal dendrites. Annu. Rev. Neurosci. *19*, 165–186.

Jones, J., and Palmer, L. (1987). An evaluation of the two-dimensional Gabor filter model of simple receptive fields in cat striate cortex. J. Neurophysiol. *58*, 1233–1258.

Jonides, J., and Gleitman, H. (1972). A conceptual category effect in visual search: O as letter or digit. Percept. Psychophys. *12*, 457–460.

Julesz, B. (1975). Experiments in the visual perception of texture. Sci. Am. *232*, 34–43.

Kahneman, D. (1973). Attention and Effort (Englewood Cliffs, NJ: Prentice-Hall).

Kahneman, D., and Henik, A. (1981). Perceptual organization and attention. In Perceptual Organization, M. Kubovy and J. Pomerantz, eds. (Hillsdale, NJ: Lawrence Erlbaum Associates).

Kahneman, D., Treisman, A., and Gibbs, B. (1992). The reviewing of object files: object-specific integration of information. Cogn. Psychol. *24*, 175–219.

Kammen, D.M., Holmes, P.J., and Koch, C. (1989). Origin of oscillations in visual cortex: feedback versus local coupling. In Models of Brain Functions, R.M.J. Cotterill, ed. (Cambridge: Cambridge University Press).

Kanisza, G. (1979). The Organization of Vision (New York: Praeger).

Kapadia, M.K., Ito, M., Gilbert, C.D., and Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys. Neuron *15*, 843–856.

Kastner, S., De Weerd, P., Desimone, R., and Ungerleider, L.G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. Science *282*, 108–111.

Kastner, S., Pinsk, M.A., De Weerd, P., Desimone, R., and Ungerleider, L.G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. Neuron *22*, 751–761.

Kefalea, E. (1998). Object localization and recognition for a grasping robot. In Proceedings of the 24th Annual Conference of the IEEE Industrial Electronics Society (Aachen, Germany).

Keil, K., Müller, M.M., Ray, W.J., Gruber, T., and Elbert, T. (1999). Human gamma band activity and perception of a Gestalt. J. Neurosci. *19*, 7152–7161.

Kersten, D. (1999). High-level vision as statistical inference. In The Cognitive Neurosciences, M.S. Gazzaniga, ed. (Cambridge, MA: MIT Press).

Kilgard, M.P., and Merzenich, M.M. (1998). Plasticity of temporal information processing in the primary auditory cortex. Nat. Neurosci. *1*, 727–731.

Kim, J.-N., and Shadlen, M.N. (1999). Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque. Nat. Neurosci. *2*, 176–185.

Kiorpes, L., and McKee, S.P. (1999). Amblyopia and its neural basis. Curr. Opin. Neurobiol., in press.

Kiorpes, L., and Movshon, J.A. (1996). Amblyopia: a developmental disorder of the central visual pathways. Cold Spring Harbor Symp. Quant. Biol. *61*, 39–48.

Kiorpes, L., Kiper, D., O'Keefe, L., Cavanaugh, J., and Movshon, J. (1998). Neuronal correlates of amblyopia in the visual cortex of macaque monkeys with experimental strabismus and anisometropia. J. Neurosci. *18*, 6411–6424.

Kiper, D.C., Gegenfurtner, K.R., and Movshon, J.A. (1996). Cortical oscillatory responses do not affect visual segmentation. Vision Res. *36*, 539–544.

Kisvarday, Z.F., Toth, E., Rausch, M., and Eysel, U.T. (1997). Orientation-specific relationship between populations of excitatory and inhibitory lateral connections in the visual cortex of the cat. Cereb. Cortex *7*, 605–618.

Kobatake, E., and Tanaka, K. (1994). Neuronal selectivities to complex object features in the ventral visual pathway of the macaque cerebral cortex. J. Neurophys. *71*, 856–857.

Kobatake, E., Wang, G., and Tanaka, K. (1998). Effects of shape-discrimination training on the selectivity of inferotemporal cells in adult monkeys. J. Neurophysiol. *80*, 324–330.

Koch, C. (1999). Biophysics of Computation (New York: Oxford University Press).

Koch, C., and Poggio, T. (1999). Predicting the visual world: silence is golden. Nat. Neurosci. *2*, 9–10.

Koch, C., and Ullman, S. (1985). Shifts in selective visual attention: towards the underlying neural circuitry. Hum. Neurobiol. *4*, 219–227.

Koch, C., Rapp, M., and Segev, I. (1996). A brief history of time (constants). Cereb. Cortex *6*, 93–101.

Koffka, K. (1935). Principles of Gestalt Psychology (New York: Harcourt, Brace and World).

Koffka, K. (1969). The Task of Gestalt Psychology (Princeton: Princeton University Press).

Köhler, W. (1930). Gestalt Psychology (London: Bell and Sons).

Köhler, W., and Held, R. (1949). The cortical correlate of pattern vision. Science *110*, 414–419.

Konen, W., and von der Malsburg, C. (1993). Learning to generalize from single examples in the dynamic link architecture. Neural Comput. *5*, 719–735.

Konen, W., Maurer, T., and von der Malsburg, C. (1994). A fast dynamic link matching algorithm for invariant pattern recognition. Neural Networks *7*, 1019–1030.

König, P., and Schillen, T.B. (1991). Stimulus-dependent assembly formation of oscillatory responses: I. Synchronization. Neural Comput. *3*, 155–166.

König, P., Engel, A.K., and Singer, W. (1996). Integrator or coincidence detector? The role of the cortical neuron revisted. Trends Neurosci. *19*, 130–137.

König, P., Engel, A.K., and Singer, W. (1995). Relation between oscillatory activity and long-range synchronization in cat visual cortex. Proc. Natl. Acad. Sci. USA *92*, 290–294.

König, P., Engel, A.K., Löwel, S., and Singer, W. (1993). Squint affects synchronization of oscillatory responses in cat visual cortex. Eur. J. Neurosci. *5*, 501–508.

Kovacs, I., and Julesz, B. (1993). A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation. Proc. Natl. Acad. Sci. USA *90*, 7495–7497.

Kreiter, A.K., and Singer, W. (1992). Oscillatory neuronal responses in the visual cortex of the awake macaque monkey. Eur. J. Neurosci. *4*, 369–375.

Kreiter, A.K., and Singer, W. (1996). Stimulus-dependent synchronization of neuronal responses in the visual cortex of the awake macaque monkey. J. Neurosci. *16*, 2381–2396.

Krüger, L.E. (1984). The category effect in visual search depends on physical rather than conceptual differences. Percept. Psychophys. *35*, 558–564.

Krüger, J., and Aiple, F. (1988). Multimicroelectrode investigation of monkey striate cortex: spike train correlations in the infragranular layers. J. Neurophysiol. *60*, 798–828.

Kwak, H., Dagenbach, D., and Egeth, H. (1991). Further evidence for a time-independent shift of the focus of attention. Percept. Psychophys. *49*, 473–480.

Lades, M., Vorbrüggen, J.C., Buhmann, J., Lange, J., von der Malsburg, C., Würtz, R., and Konen, W. (1993). Distortion invariant object recognition in the dynamic link architecture. IEEE Trans. Comput. *42*, 300–311.

Lamme, V.A. (1995). The neurophysiology of figure-ground segregation in primary visual cortex. J. Neurosci. *15*, 1605–1615.

Lamme, V.A.F., and Spekreijse, H. (1999). Neuronal synchrony does not represent texture segregation. Nature *396*, 362–366.

Lampl, I., Reichova, I., and Ferster, D. (1999). Synchronous membrane potential fluctuations in neurons of the cat visual cortex. Neuron *22*, 361–374.

Larkum, M.E., Zhu, J.J., and Sakmann, B. (1999). A new cellular mechanism for coupling inputs arriving at different cortical layers. Nature *398*, 338–341.

Lashley, K.S., Chow, K.L., and Semmes, J. (1951). An examination of the electrical field theory of cerebral integration. Psychol. Rev. *58*, 128–136.

Laufer, M., and Verzeano, M. (1967). Periodic activity in the visual system of the cat. Vision Res. *7*, 215–229.

Laurent, G. (1996). Dynamical representation of odors by oscillating and evolving neural assemblies. Trends Neurosci. *19*, 489–496.

Laurent, G., Wehr, M., and Davidowitz, H. (1996). Temporal representations of odors in an olfactory network. J. Neurosci. *16*, 3837–3847.

Lavie, N., and Driver, J. (1996). On the spatial extent of attention in object-based visual selection. Percept. Psychophys. *58*, 1238–1251.

Lee, S.-H., and Blake, R. (1999). Visual form created solely from temporal structure. Science *284*, 1165–1168.

Lee, C., Rohrer, W.H., and Sparks, D.L. (1988). Population coding of saccadic eye movements by neurons in the superior colliculus Nature *332*, 357–360.

Lee, D., Itti, L., Koch, C., and Braun, J. (1999). Attention activates winner-take-all competition among visual filters. Nat. Neurosci. *2*, 375–381.

Legendy, C. (1970). The brain and its information trapping device. In Progress in Cybernetics, Volume *1*, J. Rose, ed. (New York: Gordon and Breach).

Lennie, P. (1981). The physiological basis of variations in visual latency. Vision Res. *21*, 815–824.

Lennie, P., Krauskopf, J., and Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. J. Neurosci. *10*, 649–669.

Leon, M.I., and Shadlen, M.N. (1998). Exploring the neurophysiology of decisions. Neuron *21*, 669–672.

Leonards, U., Singer, W., and Fahle, M. (1996). The influence of temporal phase differences on texture segmentation. Vision Res. *36*, 2689–2697.

Leonards, U., and Singer, W. (1998). Two segmentation mechanisms with differential sensitivity for colour and luminance contrast. Vision Res. *38*, 101–109.

Leonards, U., Singer, W., and Fahle, M. (1996). The influence of temporal phase differences on texture segmentation. Vision Res. *36*, 2689–2697.

Leopold, D.A., and Logothetis, N.K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. Nature *379*, 549–553.

Leventhal, A.G., Thompson, K.G., Liu, D., Zhou, Y., and Ault, S.J. (1995). Concomitant sensitivity to orientation, direction, and color of cells in Layers 2, 3, and 4 of monkey striate cortex. J. Neurosci. *15*, 1808–1818.

Levi, D., and Sharma, V. (1998). Integration of local orientation in strabismic amblyopia. Vision Res. *38*, 775–781.

Levick, W.R., and Zacks, J.L. (1970). Responses of cat retinal ganglion cells to brief flashes of light. J. Physiol. (Lond.) *206*, 677–700.

Levitt, J.B., and Lund, J.S. (1997). Contrast dependence of contextual effects in primate visual cortex. Nature *387*, 73–76.

Levitt, J.B., Kiper, D.C., and Movshon, J.A. (1994). Receptive field and functional architecture of macaque V2. J. Neurophysiol. *71*, 2517–2542.

Levitt, J.B., Lund, J.S., and Yoshioka, T. (1996). Anatomical substrates for early stages in cortical processing of visual information in the macaque monkey. Behav. Brain Res. *76*, 5–19.

Li, C.-Y., and Li, W. (1994). Extensive integration field beyond the classical receptive field of cat striate cortical neurons-classification and tuning properties. Vision Res. *34*, 2337–2355.

Li, Z. (1999a). Visual segmentation by contextual influences via intracortical interactions in the primary visual cortex. Network Comput. Neural Syst. *10*, 187–212.

Li, Z. (1999b). A neural model of contour integration in the primary visual cortex. Neural Comput., in press.

Lisberger, S.G., and Movshon, J.A. (1999). Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. J. Neurosci. *19*, 2224–2246.

Lisman, J.E. (1997). Bursts as a unit of neural information: making unreliable synapses reliable. Trends Neurosci. *20*, 38–43.

Lisman, J.E., and Idiart, M.A. (1995). Storage of 7 ± 2 short-term memories in oscillatory subcycles. Science *267*, 1512–1515.

Livingstone, M.S. (1996). Oscillatory firing and interneuronal correlations in squirrel monkey striate cortex. J. Neurophysiol. *75*, 2467–2485.

Livingstone, M.S., and Hubel, D.H. (1983). Specificity of corticocortical connections in monkey visual system. Nature *304*, 531–534.

Livingstone, M.S., and Hubel, D.H. (1984). Anatomy and physiology of a color system in the primate visual cortex. J. Neurosci. *4*, 309–356.

Livingstone, M.S., and Hubel, D.H. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. Science *240*, 740–749.

Llinas, R.R. (1988). The intrinsic electrophysiological properties of mammalian neurons: insights into central nervous system function. Science *242*, 1654–1664.

Llinas, R., and Ribary, U. (1993). Coherent 40 Hz oscillation characterizes dream state in humans. Proc. Natl. Acad. Sci. USA *90*, 2078–2081.

Llinas, R.R., Grace, A.A., and Yarom, Y. (1991). In vitro neurons in mammalian cortical layer 4 exhibit intrinsic oscillatory activity in the 10- to 50-Hz frequency range. Proc. Natl. Acad. Sci. USA *88*, 897–901.

Löwel, S., and Singer, W. (1992). Selection of intrinsic horizontal connections in the visual cortex by correlated neuronal activity. Science *255*, 209–212.

Logothetis, N.K. (1998). Single units and conscious vision. Philos. Trans. R. Soc. Lond. B Biol. Sci. *353*, 1801–1818.

Logothetis, N.K., and Pauls, J. (1995). Psychophysical and physiological evidence for viewer-centered object representations in the primate. Cereb. Cortex *5*, 270–288.

Logothetis, N.K., and Schall, J.D. (1989a). Neuronal activity related to motion perception in the middle temporal (MT) visual area of the macaque. In Neural Mechanisms of Visual Perception: Proceedings of the Retina Research Foundation, D.M.-K. Lam and C.D. Gilbert, eds. (The Woodlands, TX: Portfolio Publishing Company).

Logothetis, N.K., and Schall, J.D. (1989b). Neuronal correlates of subjective visual perception. Science *245*, 761–763.

Logothetis, N.K., Pauls, J., and Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. Curr. Biol. *5*, 552–563.

Luck, S.J., and Vogel, E.K. (1997). The capacity of visual working memory for features and conjunctions. Nature *390*, 279–281.

Luck, S.J., Chelazzi, L., Hillyard, S.A., and Desimone, R. (1997a). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. J. Neurophysiol. *77*, 24–42.

Luck, S.J., Girelli, M., McDermott, M.T., and Ford, M.A. (1997b). Bridging the gap between monkey neurophysiology and human perception: an ambiguity resolution theory of visual selective attention. Cogn. Psychol. *33*, 64–87.

Lumer, E.D., Edelman, G.M., and Tononi, G. (1997a). Neural dynamic in a model of the thalamocortical system. I. Layers, loops and the emergence of fast synchronous rhythms. Cereb. Cortex *7*, 207–227.

Lumer, E.D., Edelman, G.M., and Tononi, G. (1997b). Neural dynamics in a model of the thalamocortical system. II. The role of neural synchrony tested through perturbations of spike timing. Cereb. Cortex *7*, 228–236.

Luthi, A., and McCormick, D.A. (1998). H-current: properties of a neuronal and network pacemaker. Neuron *21*, 9–12.

Lytton, W.W., and Sejnowski, T.J. (1991). Simulations of cortical pyramidal neurons synchronized by inhibitory interneurons. J. Neurophysiol. *66*, 1059–1079.

MacLeod, K., and Laurent, G. (1996). Distinct mechanisms for synchronization and temporal patterning of odor-encoding neural assemblies. Science *274*, 976–979.

MacLeod, K., Backer, A., and Laurent, G. (1998). Who reads temporal information contained across synchronized and oscillatory spike trains? Nature *395*, 693–698.

Madler, C., and Pöppel, E. (1987). Auditory evoked potentials indicate the loss of neuronal oscillations during general anesthesia. Naturwissenschaften *74*, 42–43.

Magee, J.C., and Johnston, D.A. (1997). A synaptically controlled, associative signal for Hebbian plasticity in hippocampal neurons. Science *275*, 209–213.

Mainen, Z.F., and Sejnowski, T.J. (1995). Reliability of spike timing in neocortical neurons. Science *268*, 1503–1506.

Malach, R., Amir, Y., Harel, M., and Grinvald, A. (1993). Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex. Proc. Natl. Acad. Sci. USA *90*, 10469–10473.

Maldonado, P.E., Friedman-Hill, S.R., and Gray, C.M. (1999). Temporal dynamics of neuronal activity in the striate cortex of alert macaque: II. Short and long-range temporally-correlated activity. J. Neurosci., in press.

Marcelja, S. (1980). Mathematical description of the responses of simple cortical cells. J. Optic. Soc. Am. *70*, 1297–1300.

Margulis, M., and Tang, C.-M. (1998). Temporal integration can readily switch between sublinear and supralinear summation. J. Neurophysiol. *79*, 2809–2813.

Markram, H., Lübke, J., Frotscher, M., and Sakmann, B. (1997). Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs. Science *275*, 213–215.

Marr, D. (1982). Vision (San Francisco: Freeman).

Marsalek, P., Koch, C., and Maunsell, J.H.R. (1997). On the relationship between synaptic input and spike output jitter in individual neurons. Proc. Natl. Acad. Sci. USA *94*, 735–740.

Mason, A., Nicoll, A., and Stratford, K. (1991). Synaptic transmission between individual pyramidal neurons of the rat visual cortex in vitro. J. Neurosci. *11*, 72–84.

Massad, A., Mertsching, B., and Schmalz, S. (1998). Combining multiple views and temporal associations for 3-D object recognition. In Proceedings of the ECCV 1998, Volume 2 Stockholm.

Matsumura, M., Chen, D.-F., Sawaguchi, T., Kubota, K., and Fetz, E.E. (1996). Synaptic interactions between primate precentral cortex neurons revealed by spike-triggered averaging of intracellular membrane potentials in vivo. J. Neurosci. *16*, 7757–7767.

Maunsell, J.H.R., and Gibson, J.R. (1992). Visual response latencies in striate cortex of the macaque monkey. J. Neurophysiol. *68*, 1332–1344.

Maunsell, J.H.R., and Newsome, W.T. (1987). Visual processing in monkey extrastriate cortex. Annu. Rev. Neurosci. *10*, 363–401.

Maunsell, J.H., Sclar. G., Nealey, T.A., and DePriest, D.D. (1991). Extraretinal representations in area V4 in the macaque monkey. Vis. Neurosci. *7*, 561–573.

Maunsell, J.H.R., Ghose, G.M., Assad, J.A., McAdams, C.J., Boudreau, C.E., and Noerager, B.D. (1999). Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. Vis. Neurosci. *16*, 1–14.

McAdams, C.J., and Maunsell, J.H.R. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. J. Neurosci. *19*, 431–441.

McClelland, J.L., and Mozer, M.C. (1986). Perceptual interactions in two-word displays: familiarity and similarity effects. J. Exp. Psychol. Hum. Percept. Perform. *12*, 18–35.

McCollough, C. (1965). Color adaptation of edge-detectors in the human visual system. Science *149*, 1115–1116.

McCulloch, W., and Pitts, W. (1943). A logical calculus of the ideas immanent in nervous activity. Bull. Math. Biophys. *5*, 115–133.

McCormick, D.A., Connors, B.W., Lighthall, J.W., and Prince, D.A. (1985). Comparative electrophysiology of pyramidal and sparsely spiny stellate neurons of the neocortex. J. Neurophysiol. *54*, 782–806.

McLeod, P., Driver, J., and Crisp, J. (1988). Visual search for conjunctions of movement and form is parallel. Nature *332*, 154–155.

McLeod, P., Driver, J., Dienes, Z., and Crisp, J. (1991). Filtering by movement in visual search. J. Exp. Psychol. Hum. Percept. Perform. *17*, 55–64.

Mel, B., and Fiser, J. (1999). Minimizing binding errors using learned conjunctive features. Neural Comput., in press.

Melssen, W.J., and Epping, W.J.M. (1987). Detection and estimation of neural connectivity based on cross correlation analysis. Biol. Cybern. *57*, 403–414.

Merigan, W.H., and Maunsell, J.H. (1993). How parallel are the primate visual pathways? Annu. Rev. Neurosci. *16*, 369–402.

Michalski, A., Gerstein, G.L., Czarkowska, J., and Tarnecki, R. (1983). Interactions between cat striate cortex neurons. Exp. Brain Res. *51*, 97–107.

Mikami, A., Newsome, W.T., and Wurtz, R.H. (1986). Motion selectivity in macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT. J. Neurophysiol. *55*, 1308–1327.

Miles, R., and Wong, R.K.S. (1986). J. Physiol. *380*, 373–397.

Miller, E.C., Gochin, P.M., and Gross, C.G. (1993). Suppression of visual responses of neurons in inferior temporal cortex of the awake macaque monkey by addition of a second stimulus. Brain Res. *616*, 25–29.

Milner, P. (1974). A model for visual shape recognition. Psychol. Rev. *81*, 521–535.

Milner, A.D., and Goodale, M.A. (1993). Visual pathways to perception and action. Prog. Brain Res. *95*, 317–337.

Miltner, W.H.R., Braun, C, Arnold, M., Witte, H., and Taub, E. (1999). Coherence of gamma-band EEG activity as a basis for associative learning. Nature *397*, 434–436.

Minsky, M. (1961). Steps toward artificial intelligence. Proc. Inst. Radio Engr. *49*, 8–30.

Missal, M., Vogels, R., and Orban, G. (1997). Responses of macaque inferior temporal neurons to overlapping shapes. Cereb. Cortex *7*, 758–767.

Moore, G.P., Segundo, J.P., Perkel, D.H., and Levitan, H. (1970). Statistical signs of synaptic interactions in neurones. Biophys. J. *10*, 876–900.

Moran, J., and Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. Science *229*, 782–784.

Motter, B.C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. J. Neurophysiol. *70*, 909–919.

Motter, B.C., and Mountcastle, V.B. (1981). The functional properties of the light-sensitive neurons of the posterior parietal cortex studied in waking monkeys: foveal sparing and opponent vector organization. J. Neurosci. *1*, 3–26.

Mountcastle, V.B. (1978). An organizing principle for cerebral function: the unit module and the distributed system. In The Mindful Brain, G.M. Edelman and V.B. Mountcastle, eds. (Cambridge, MA: MIT Press).

Movshon, J.A., Adelson, E.H., Gizzi, M.S., and Newsome, W.T. (1985). The analysis of moving visual patterns. Exp. Brain Res. *11*, 117–151.

Movshon, J., Eggers, H., Gizzi, M., Hendrickson, A., Kiorpes, L., and Boothe, R. (1987). Effects of early unilateral blur on the macaque's visual system. III. Physiological observations. J. Neurosci. *7*, 1340–1351.

Mozer, M.C. (1983). Letter migration in word perception. J. Exp. Psychol. Hum. Percept. Perform. *9*, 531–546.

Mozer, M. (1991). The Perception of Multiple Objects: A Connectionist Approach (Cambridge, MA: MIT Press).

Munk, M.H.J., Roelfsema, P.R., König, P., Engel, A.K., and Singer, W. (1996). Role of reticular activation in the modulation of intracortical synchronization. Science *272*, 271–274.

Murata, A., Gallese, V., Kaseda, M., and Sakata, H. (1996). Parietal neurons related to memory-guided hand manipulation. J. Neurophysiol. *75*, 2180–2186.

Murthy, V.N., and Fetz, E.E. (1996a). Oscillatory activity in sensorimotor cortex of awake monkeys: synchronization of local field potentials and relation to behavior. J. Neurophysiol. *76*, 3949–3967.

Murthy, V.N., and Fetz, E.E. (1996b). Synchronization of neurons during local field potential oscillations in sensorimotor cortex of awake monkeys. J. Neurophysiol. *76*, 3968–3682.

Nakayama, K., and Silverman, G.H. (1986a). Serial and parallel processing of visual feature conjunctions. Nature *320*, 264–265.

Navon, D. (1975). Forest before trees: the precedence of global features in visual perception. Cogn. Psychol. *9*, 353–383.

Neisser, U. (1963). Decision-time without reaction-time: experiments in visual scanning. Am. J. Psychol. *76*, 376–385.

Neisser, U. (1967). Cognitive Psychology (New York: Appleton-Century-Crofts).

Neisser, U., and Becklen, R. (1975). Selective looking: attending to visually specified events. Cogn. Psychol. *7*, 480–494.

Nelson, J.I., Salin, P.A., Munk, M.H.J., Arzi, M., and Bullier, J. (1992). Spatial and temporal coherence in cortico-cortical connections: a cross-correlation study in areas 17 and 18 in the cat. Vis. Neurosci. *9*, 21–38.

Neuenschwander, S., and Singer, W. (1996). Long-range synchronization of oscillatory light responses in the cat retina and lateral geniculate nucleus. Nature *379*, 728–733.

Neuenschwander, S., Castelo-Branco, M., and Singer, W. (1999). Synchronous oscillations in the cat retina. Vision Res. *39*, 2485–2497.

Neven, H., and Aertsen, A. (1992). Rate coherence and event coherence in the visual cortex: a neuronal model of object recognition. Biol. Cybern. *67*, 309–322.

Newsome, W.T., Britten, K.H., and Movshon, J.A. (1989). Neuronal correlates of a perceptual decision. Nature *341*, 52–54.

Nicolelis, M.A.L., and Chapin, J.K. (1994). Spatiotemporal structure of somatosensory responses of many-neuron ensembles in the rat ventral posterior medial nucleus of the thalamus. J. Neurosci. *14*, 3511–3532.

Nicolelis, M.A., Ghazanfar, A.A., Stambaugh, C.R., Oliveira, L.M., Laubach, M., Chapin, J.K., Nelson, R.J., and Kaas, J.H. (1998). Simultaneous encoding of tactile information by three primate cortical areas. Nat. Neurosci. *1*, 621–630.

Nicoll, A., and Blakemore, C. (1993). Single-fiber EPSPs in layer 5 of rat visual cortex in-vitro. Neuroreport *4*, 167–170.

Niebur, E., Kammen, D.M., and Koch, C. (1990). Phase-locking in 1-D and 2-D networks of oscillating neurons. In Nonlinear Dynamics and Neuronal Networks, H.G. Schuster, ed. (Weinheim: VCH Publishers).

Niebur, E., Koch, C., and Rosin, C. (1993). An oscillation-based model for the neuronal basis of attention. Vision Res. *33*, 2789–2802.

Nobre, A.C., Sebestyen, G.N., Gitelman, D.R., Mesulam, M.M., Frackowiak, R.S., and Frith, C.D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. Brain *120*, 515–533.

Nothdurft, H.C. (1992). Feature analysis and the role of similarity in pre-attentive vision. Percept. Psychophys. *52*, 355–375.

Nothdurft, H.C. (1993). Faces and facial expression do not pop-out. Perception *22*, 1287–1298.

Nowak, L.G., Munk, M.H., Girard, P., and Bullier, J. (1995a). Visual latencies in areas V1 and V2 of the macaque monkey. Vis. Neurosci. *12*, 371–384.

Nowak, L.G., Munk, M.H., Nelson, J.I., James, A.C., and Bullier, J. (1995b). Structural basis of cortical synchronization. I. Three types of interhemispheric coupling. J. Neurophysiol. *74*, 2379–2400.

Nowak, L.G., Munk, M.H., James, A.C., Girard, P., and Bullier, J. (1999). Cross-correlation study of the temporal interactions between areas V1 and V2 of the macaque monkey. J. Neurophysiol. *81*, 1057–1074.

Nowlan, S., and Sejnowski, T. (1995). A selection model for motion processing in area MT of primates. J. Neurosci. *15*, 1195–1214.

Okada, K, Steffens J., Maurer, T., Hong, H., Elagin, E., Neven, H., and von der Malsburg, C (1998). The Bochum/USC face recognition system and how it fared in the FERET phase III test. In Face Recognition: From Theory to Applications, H. Wechsler, P.J. Phillips, V. Bruce, F. Fogelman-Souli, and T.S. Huang, eds. (New York: Springer-Verlag).

O'Keefe, L.P., and Movshon, J.A. (1998). Processing of first- and second-order motion signals by neurons in area MT of the macaque monkey. Vis. Neurosci. *15*, 305–317.

Oliva, A., and Schyns, P.G. (1997). Coarse blobs or fine edges? Evidence that information diagnosticity changes the perception of complex visual stimuli. Cogn. Psychol. *34*, 72–107.

Olshausen, B.A., Anderson, C.H., and Van Essen, D.C. (1993). A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. J. Neurosci. *13*, 4700–4719.

Olshausen, B., Anderson, C., and Van Essen, D. (1995). A multiscale dynamic routing circuit for forming size- and position-invariant object representations. J. Comput. Neurosci. *2*, 45–62.

Orban, G.A., Kennedy, H., and Bullier, J. (1986). Velocity sensitivity and direction selectivity of neurons in areas V1 and V2 of the monkey: influence of eccentricity. J. Neurophysiol. *56*, 462–480.

Pal, N.R., and Pal, S.K. (1993). A review of image segmentation techniques. Pattern Recog. Lett. *26*, 1277–1294.

Palm, G. (1981). Towards a theory of cell assemblies. Biol. Cybern. *39*, 181–194.

Palm, G. (1990). Cell assemblies as a guideline for brain research. Concepts Neurosci. *1*, 133–137.

Palm, G., Aertsen, A., and Gerstein, G.L. (1988). On the significance of correlations among neuronal spike trains. Biol. Cybern. *59*, 1–11.

Parker, A.J., and Newsome, W.T. (1998). Sense and the single neuron: probing the physiology of perception. Annu. Rev. Neurosci. *21*, 227–277.

Perkel, D.H., Gerstein, G.L., and Moore, G.P. (1967). Neuronal spike trains and stochastic point processes. I. The single spike train. Biophys. J. *7*, 391–418.

Perrett, D., and Oram, M. (1993). Neurophysiology of shape processing. Imag. Vis. Comput. *11*, 317–333.

Perrett, D., and Oram, M. (1998). Visual recognition based on temporal cortex cells: viewer-centred processing of pattern configuration. Z. Naturforsch. *53c*, 518–541.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1984). Neurones responsive to faces in the temporal cortex: studies of functional organization, sensitivity to identity and relation to perception. Hum. Neurobiol. *3*, 197–208.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. Proc. R. Soc. Lond. B Biol. Sci. *223*, 293–317.

Perrett, D.I., Mistlin, A.J., and Chitty, A.J. (1987). Visual neurones responsive to faces. Trends Neurosci. *10*, 358–364.

Perrett, D., Oram, M., Harries, M., Bevan, R., Hietanen, J., Benson, P., and Thomas, S. (1991). Viewer-centred and object-centred coding of heads in the macaque temporal cortex. Exp. Brain Res. *86*, 159–173.

Peterhans, E., and von der Heydt, R. (1993). Functional organization of area V2 in the alert macaque. J. Neurosci. *5*, 509–524.

Peters, A., and Sethares, C. (1991). Organization of pyramidal neurons in area 17 of monkey visual cortex. J. Comp. Neurol. *306*, 1–23.

Peters, A., and Yilmaz, E. (1993). Neuronal organization in area 17 of cat visual cortex. Cereb. Cortex *3*, 49–68.

Phillips, W.A., and Singer, W. (1997). In search of common foundations for cortical computation. Behav. Brain Sci. *20*, 657–722.

Phillips, W.A., Hancock, P.J.B., Willson, N.J., and Smith, L.S. (1988). On the acquisition of object concepts from sensory data. In Neural Computers. R. Eckmiller and C. von der Malsburg, eds. (Heidelberg: Springer).

Phillips, P.J., Moon, H., Rizvi, S., and Rauss, P. (1998). The FERETE valuation. In Face Recognition: From Theory to Applications. H. Wechsler, P.J. Phillips, V. Bruce, F. Fogelman-Souli, and T.S. Huang, eds. (New York: Springer-Verlag).

Platt, M.L., and Glimcher, P.W. (1997). Responses of intraparietal neurons to saccadic targets and visual distractors. J. Neurophysiol. *78*, 1574–1589.

Plenz, D., and Kitai, S.T. (1996). Generation of high-frequency oscillations in local circuits of rat somatosensory cortex cultures. J. Neurophysiol. *76*, 4180–4184.

Poggio, T., and Edelman, S. (1990). A network that learns to recognize 3D objects. Nature *343*, 263–266.

Poggio, G.F., and Fischer, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. J. Neurophysiol. *40*, 1392–1405.

Poggio, T., Reichardt, W., and Hausen, W. (1981). A neuronal circuitry for relative movement discrimination by the visual system of the fly. Naturwissenschaften *68*, 443–466.

Polat, U., Sagi, D., and Norcia, A. (1997). Abnormal long-range spatial interactions in amblyopia. Vision Res. *37*, 737–744.

Polat, U., Mizobe, K., Pettet, M.W., Kasamatsu, T., and Norcia, A.M. (1998). Collinear stimuli regulate visual responses depending on a cell's contrast threshold. Nature *391*, 580–584.

Pomerantz, J. (1981). Perceptual organization in information processing. In Perceptual Organization, M. Kubovy and J. Pomerantz, eds. (Hillsadle, NJ: Lawrence Erlbaum Associates).

Potter, M. (1975). Meaning in visual search. Science *187*, 565–566.

Potter, M.C., and Levy, E.I. (1969). Recognition memory for a rapid sequence of pictures. J. Exp. Psychol. *81*, 10–15.

Pouget, A., and Sejnowski, T.J. (1997). A new view of hemineglect based on the response properties of parietal neurones. Philos. Trans. R. Soc. Lond. B Biol. Sci. *352*, 1449–1459.

Prinzmetal, W. (1981). Principles of feature integration in visual perception. Percep. Psychophys. *30*, 330–340.

Prinzmetal, W., and Keysar, B. (1989). Functional theory of illusory conjunctions and neon colors. J. Exp. Psychol. Gen. *118*, 165–190.

Prinzmetal, W., Presti, D.E., and Posner, M.I. (1986). Does attention affect visual feature integration? J. Exp. Psychol. Hum. Percept. Perform. *12*, 361–369.

Prinzmetal, W., Henderson, D., and Ivry, R. (1995). Loosening the constraints on illusory conjunctions: assessing the roles of exposure duration and attention. J. Exp. Psychol. Hum. Percept. Perform. *21*, 1362–1375.

Prut, Y., Vaadia, E., Bergman, H., Haalman, I., Slovin, H., and Abeles, M. (1998). Spatiotemporal structure of cortical activity: properties and behavioral relevance. J. Neurophysiol. *7*, 2857–2874.

Pulvermüller, F., Birbaumer, N., Lutzenberger, W., and Mohr, B. (1997). High frequency brain activity: its possible role in attention, perception and language processing. Prog. Neurobiol. *52*, 427–445.

Purves, D., and LaMantia, A.-S. (1990). Number of 'blobs' in the primary visual cortex of neonatal and adult monkeys. Proc. Natl. Acad. Sci. USA *87*, 5764–5767.

Qian, N., and Andersen, R.A. (1994). Transparent motion perception as detection of unbalanced motion signals. II. Physiology. J. Neurosci. *14*, 7367–7380.

Quinlan, P.T., and Humphreys, G.W. (1987). Visual search for targets defined by combinations of color, shape, and size: an examination of the task constraints on feature and conjunction searches. Percept. Psychophys. *41*, 455–472.

Rafal, R.D. (1997). Balint syndrome. In Behavioral neurology and Neuropsychology, T.E. Feinberg and M.J. Farah, eds. (New York: McGraw-Hill).

Rager, G., and Singer, W. (1998). The response of cat visual cortex to flicker stimuli of variable frequency. Eur. J. Neurosci. *10*, 1856–1877.

Raiguel, S.E., Lagae, L., Gulyas, B., and Orban, G.A. (1989). Response latencies of visual cells in macaque areas V1, V2 and V5. Brain Res. *493*, 155–159.

Rainer, G., Asaad, W.F., and Miller, E.K. (1998). Memory fields of neurons in the primate prefrontal cortex. Proc. Natl. Acad. Sci. USA *95*, 15008–15013.

Recanzone, G.H., Wurtz, R.H., and Schwarz, U. (1997). Responses of MT and MST neurons to one and two moving objects in the receptive field. J. Neurophysiol. *78*, 2904–2915.

Reitboeck, H.J., Eckhorn, R., and Pabst, M. (1987). A model of figure/ground separation based on correlated neural activity in the visual system. In Synergetics of the Brain, H. Haken, ed. (New York: Springer).

Rensink, R.A., and Enns, J.T. (1995). Preemption effects in visual search: evidence for low-level grouping. Psychol. Rev. *102*, 101–130.

Reyes, A.D., and Fetz, E.E. (1993). Two modes of interspike interval shortening by brief transient depolarizations in cat neocortical neurons. J. Neurophysiol. *69*, 1661–1672.

Reyes, A., Rubel, E., and Spain, W. (1994). Membrane properties underlying the firing of neurons in the avian cochlear nucleus. J. Neurosci. *14*, 5352–5364.

Reyes, A., Rubel, E., and Spain, W. (1996). In vitro analysis of optimal stimuli for phase-locking and time-delayed modulation of firing in avian nucleus laminaris neurons. J. Neurosci. *16*, 993–1007.

Reynolds, J.H., and Desimone, R. (1999). The role of neural mechanisms of attention in solving the binding problem. Neuron *24*, this issue, 19–29.

Reynolds, J., Chelazzi, L., and Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. J. Neurosci. *19*, 1736–1753.

Rhodes, P., and Gray, C.M. (1994). Simulations of intrinsically bursting neocortical pyramidal neurons. Neural Comput. *6*, 1086–1110.

Ribary, U., Joannides, A.A., Singh, K.D., Hasson, R., Bolton, J.P.R., Lado, F., Mogilner, A., and Llinas, R. (1991). Magnetic field tomography of coherent thalamocortical 40 Hz oscillations in humans. Proc. Natl. Acad. Sci. USA *88*, 11037–11041.

Riehle, A., Grun, S., Diesmann, M., and Aertsen, A. (1997). Spike synchronization and rate modulation differentially involved in motor cortical function. Science *278*, 1950–1953.

Riesenhuber, M., and Poggio, T. (1998a). Just one view: invariances in inferotemporal cell tuning. In Advances in Neural Information Processing Systems, Volume 10, M. Jordan, M. Kearns, and S. Solla, eds. (Cambridge, MA: MIT Press).

Riesenhuber, M., and Poggio, T. (1998b). Modeling Invariances in Inferotemporal Cell Tuning, Technical Report 1629 (Cambridge, MA: MIT Artificial Intelligence Laboratory).

Riesenhuber, M., and Poggio, T. (1999a). Are cortical models really bound by the "binding problem"? Neuron *24*, this issue, 87–93.

Riesenhuber, M., and Poggio, T. (1999b). Hierarchical models of object recognition in cortex. Nat. Neurosci., in press.

Rizzolatti, G., Fogassi, L., and Gallese, V. (1997). Parietal cortex: from sight to action. Curr. Opin. Neurobiol. *7*, 562–567.

Robertson, L., Treisman, A., Freidman-Hill, S., and Grabowecky, M. (1997). The interaction of spatial and object pathways: evidence from Balint's syndrome. J. Cogn. Neurosci. *9*, 254–276.

Rock, I., and Brosgole, L. (1964). Grouping based on phenomenal proximity. J. Exp. Psychol. *67*, 531–538.

Rockel, A.J., Hiorns, R.W., and Powell, T.P.S. (1980). The basic uniformity in structure of the neocortex. Brain *103*, 221–244.

Rockland, K.S. (1997). Elements of cortical architecture: hierarchy revisited. In Cerebral Cortex: Extrastriate Cortex in Primate, K. Rockland, J. Kaas, and A. Peters, eds. (New York: Plenum Publishing Corporation).

Rockland, K.S., and Lund, J.S. (1982). Widespread periodic intrinsic connections in the tree shrew visual cortex. Science *215*, 1532–1534.

Rockland, K.S., and Van Hoesen, G.W. (1994). Direct temporal-occipital feedback connections to striate cortex (V1) in the macaque monkey. Cereb. Cortex *4*, 300–313.

Rodman, H.R., and Albright, T.D. (1989). Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). Exp. Brain Res. *75*, 53–64.

Rodriguez, E., George, N., Lachaux, J.-P., Martinerie, J., Renault, B., and Varela, F.J. (1999). Perception's shadow: long-distance gamma band synchronization of human brain activity. Nature *397*, 430–433.

Roe, A.W., and Ts'o, D.Y. (1995). Visual topography in primate V2: multiple representation across functional stripes. J. Neurosci. *15*, 3689–3715.

Roelfsema, P.R., and Singer, W. (1998). Detecting connectedness. Cereb. Cortex *8*, 385–396.

Roelfsema, P.R., König, P., Engel, A.K., Sireteanu, R., and Singer, W. (1994). Reduced synchronization in the visual cortex of cats with strabismic amblyopia. Eur. J. Neurosci. *6*, 1645–1655.

Roelfsema, P.R., Engel, A.K., König, P., and Singer, W. (1996). The role of neuronal synchronization in response selection: A biologically plausible theory of structured representations in thevisual cortex. J. Cogn. Neurosci. *8*, 603–625.

Roelfsema, P.R., Engel, A.K., König, P., and Singer, W. (1997). Visuomotor integration is associated with zero time-lag synchronization among cortical areas. Nature *385*, 157–161.

Rolls, D.T., and Tovee, M.J. (1994). Processing speed in the cerebral cortex and the neurophysiology of visual masking. Proc. R. Soc. Lond. B Biol. Sci. *257*, 9–15.

Rolls, E., and Tovee, M. (1995). The responses of single neurons in the temporal visual cortical areas of the macaque when more than one stimulus is present in the receptive field. Exp. Brain Res. *103*, 409–420.

Rosenblatt, F. (1961). Principles of Neurodynamics: Perceptions and the Theory of Brain Mechanisms. (Washington, CD: Spartan Books).

Rosenquist, A.C. (1985). Connections of visual cortical areas in the cat. In Cerebral Cortex, A. Peters and E.G. Jones, eds. (New York: Plenum Press).

Rougeul, A., Bouyer, J.J., Dedet, L., and Debray, O. (1979). Fast somato-parietal rhythms during combined focal attention and immobility in baboon and squirrel monkey. Electroenceph. Clin. Neurophysiol. *46*, 310–319.

Saarinen, J. (1996a). Localization and discrimination of "pop-out" target. Vision Res. *36*, 313–316.

Saarinen, J. (1996b). Target localization and identification in rapid visual search. Perception *25*, 305–312.

Sagi, D., and Julesz, B. (1985). "Where" and "what" in vision. Science *228*, 1217–1219.

Saito, H., Yukie, M., Tanaka, K., Hikosaka, K., Fukada, Y., and Iwai, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. J. Neurosci. *6*, 145–157.

Sakai, K., and Miyashita, Y. (1991). Neural organization for the long-term memory of paired associates. Nature *354*, 152–155.

Sakai, K., and Miyashita, Y. (1994). Neuronal tuning to learned complex forms in vision. Neuroreport *5*, 829–832.

Sakata, H., Taira, M., Murata, A., and Mine, S. (1995). Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. Cereb. Cortex *5*, 429–438.

Salin, P.A., and Bullier, J. (1995). Corticocortical connections in the visual system: structure and function. Physiol. Rev. *75*, 107–154.

Sanes, J.N., and Donoghue, J.P. (1993). Oscillations in local field potentials of the primate motor cortex during voluntary movement. Proc. Natl. Acad. Sci. USA *90*, 4470–4474.

Sato, T. (1989). Interactions of visual stimuli in the receptive fields of inferior temporal neurons in awake monkeys. Exp. Brain Res. *77*, 23–30.

Schein, S.J., and Desimone, R. (1990). Spectral properties of V4 neurons in the macaque. J. Neurosci. *10*, 3369–3389.

Schein, S.J., Marrocco, R.T., and de Monasterio, F.M. (1982). Is there a high concentration of color-selective cells in area V4 of monkey visual cortex? J. Neurophysiol. *47*, 193–213.

Schiller, J., Schiller, Y., Stuart, G., and Sakmann, B. (1997). Calcium action potentials restricted to distal apical dendrites of rat neocortical pyramidal neurons. J. Physiol. *505*, 605–616.

Schmidt, K.E., Goebel, R., Löwel, S., and Singer, W. (1997a). The perceptual grouping criterion of collinearity is reflected by anisotropies of connections in the primary visual cortex. Eur. J. Neurosci. *9*, 1083–1089.

Schmidt, K.E., Kim, D.-S., Singer, W., Bonhoeffer, T., and Löwel, S. (1997b). Functional specificity of long-range intrinsic and interhemispheric connections in the visual cortex of strabismic cats. J. Neurosci. *17*, 5480–5492.

Schmolesky, M.T., Wang, Y., Hanes, D.P., Thompson, K.G., Leutgeb, S., Schall, J.D., and Leventhal, A.G. (1998). Signal timing across the macaque visual system. J. Neurophysiol. *79*, 3272–3278.

Schroeder, C.E., Mehta, A.D., and Givre, S.J. (1998). A spatiotemporal profile of visual system activation revealed by current source density analysis in the awake macaque. Cereb. Cortex *8*, 575–592.

Schuster, H.G., and Wagner, P. (1990). A model for neuronal oscillations in the visual cortex. 2. Phase description of the feature dependent synchronization. Biol. Cybern. *64*, 83–85.

Schwarz, C., and Bolz, J. (1991). Functional specificity of the long-range horizontal connections in cat visual cortex: a cross-correlation study. J. Neurosci. *11*, 2995–3007.

Schwindt, P.C., and Crill, W.E. (1995). Amplification of synaptic current by persistent sodium conductance in apical dendrite of neocortical neurons. J. Neurophysiol. *74*, 2220–2224.

Seidemann, E., and Newsome, W.T. (1999). Effect of spatial attention on the responses of area MT neurons. J. Neurophysiol. *81*, 1783–1794.

Sejnowski, T.J. (1981). Skeleton filters in the brain. In Parallel Models of Associative Memory, G.E. Hinton and J.A. Anderson, eds. (Hillsdale, NJ: Lawrence Erlbaum Associates).

Sereno, M.I., and Allman, J.M. (1991). Cortical visual areas in mammals. In The Neural Basis of Visual Function, A. Leventhal, ed. (New York: MacMillan).

Sereno, A.B., and Maunsell, J.H.R. (1998). Shape selectivity in primate lateral intraparietal cortex. Nature *395*, 500–503.

Sestokas, A.K., and Lehmkuhle, S. (1988). Response variability of X- and Y-cells in the dorsal lateral geniculate nucleus of the cat. J. Neurophysiol. *59*, 317–325.

Shadlen, M.N., and Movshon, J.A. (1999). Synchrony unbound: a critical evaluation of the temporal bining hypothesis. Neuron *24*, this issue, 67–77.

Shadlen, M.N., and Newsome, W.T. (1994). Noise, neural codes and cortical organization. Curr. Opin. Neurobiol. *4*, 569–579.

Shadlen, M., and Newsome, W. (1995). Is there a signal in the noise? Curr. Opin. Neurobiol. *5*, 248–250.

Shadlen, M.N., and Newsome, W.T. (1996). Motion perception: seeing and deciding. Proc. Natl. Acad. Sci USA *93*, 628–633.

Shadlen, M.N., and Newsome, W.T. (1998). The variable discharge of cortical neurons: implications for connectivity, computation, and information coding. J. Neurosci. *18*, 3870–3896.

Shastri, L., and Ajjanagadde, V. (1993). From simple associations to systematic reasoning. Behav. Brain Sci. *16*, 417–494.

Sheinberg, D.L., and Logothetis, N.K. (1997). The role of temporal cortical areas in perceptual organization. Proc. Natl. Acad. Sci. USA *94*, 3408–3413.

Shimojo, S., Silverman, G.H., and Nakayama, K. (1989). Occlusion and the solution to the aperture problem for motion. Vision Res. *29*, 619–626.

Sillito, A.M., Grieve, K.L., Jones, H.L., Cuderio, J., and Davis, J. (1995). Visual cortical mechanisms detecting focal orientation discontinuities. Nature *378*, 492–496.

Silverman, M.S., Grosof, D.H., DeValois, R.L., and Elfar, S.D. (1989). Spatial-frequency organization in primate striate cortex. Proc. Natl. Acad. Sci. USA *86*, 711–715.

Simons, D.J., and Levin, D.T. (1997). Change blindness. Trends Cogn. Sci. *1*, 261–268.

Singer, W. (1993). Synchronization of cortical activity and its putative role in information processing and learning. Annu. Rev. Physiol. *55*, 349–374.

Singer, W. (1994). Putative functions of temporal correlations in neocortical processing. In Large-Scale Neuronal Theories of the Brain, C. Koch and J.L. Davis, eds. (Cambridge, MA: MIT Press).

Singer, W. (1995). Development and plasticity of cortical processing architectures. Science *270*, 758–764.

Singer, W. (1999a). Response synchronization: a universal coding strategy for the definition of relations. In The Cognitive Neurosciences, M.S. Gazzaniga, ed. (Cambridge, MA: MIT Press).

Singer, W. (1999b). Neuronal synchrony: a versatile code for the definition of relations? Neuron *24*, this issue, 49–65.

Singer, W., and Gray, C.M. (1995). Visual feature integration and the temporal correlation hypothesis. Annu. Rev. Neurosci. *18*, 555–586.

Singer, W., Engel, A.K., Kreiter, A.K., Munk, M.H.J., Neuenschwander, S., and Roelfsema, P.R. (1997). Neuronal assemblies: necessity, signature and detecability. Trends Cogn. Sci. *1*, 252–261.

Skottun, B.C., Bradley, A., Sclar, G., Ohzawa, I., and Freeman, R.D. (1987). The effects of contrast on visual orientation and spatial frequency discrimination: a comparison of single cells and behavior. J. Neurophysiol. *57*, 773–786.

Snyder, L.H., Batista, A.P., and Andersen, R.A. (1997). Coding of intention in the posterior parietal cortex. Nature *386*, 167–170.

Sompolinsky, H., Golomb, D., and Kleinfeld, D. (1990). Global processing of visual stimuli in a neural network of coupled oscillators. Proc. Natl. Acad. Sci. USA *87*, 7200–7204.

Sperry, R.W., Miner, N., and Myers, R.E. (1955). Visual pattern perception following subpial slicing and tantalum wire implantations in the visual cortex. J. Comp. Physiol. Psychol. *48*, 50–58.

Spitzer, H., Desimone, R., and Moran, J. (1988). Increased attention enhances both behavioral and neuronal performance. Science *240*, 338–340.

Sporns, O., Gally, J.A., Reeke, G.N., and Edelman, G.M. (1989). Reentrant signaling among simulated neuronal groups leads to coherency in their oscillatory activity. Proc. Natl. Acad. Sci. USA *86*, 7265–7269.

Sporns, O., Tononi, G., and Edelman, G.M. (1991). Modeling perceptual grouping and figure ground segregation by means of active reentrant connections. Proc. Natl. Acad. Sci. USA *88*, 129–133.

Stemmler, M., Usher, M., and Niebur, E. (1995). Lateral interactions in primary visual cortex: a model bridging physiology and psychophysics. Science *269*, 1877–1880.

Steriade, M., Timofeev, I., Durmuller, N., and Grenier, F. (1998). Dynamic properties of corticothalamic neurons and local cortical interneurons generating fast rhythmic (30–40 Hz) spike-bursts. J. Neurophysiol. *79*, 483–490.

Steriade, M. (1999). Coherent oscillations and short-term plasticity in corticothalamic networks. Trends Neurosci. *22*, 337–345.

Stevens, C.F., and Wang, Y. (1995). Facilitation and depression at single central synapses. Neuron *14*, 795–802.

Stevens, C.F., and Zador, A.M. (1998). Input synchrony and the irregular firing of cortical neurons. Nat. Neurosci. *1*, 210–217.

Stoner, G.R., and Albright, T.D. (1992). Neural correlates of perceptual motion coherence. Nature *358*, 412–414.

Stoner, G.R., Albright, T.D., and Ramachandran, V.S. (1990). Transparency and coherence in human motion perception. Nature *344*, 153–155.

Stopfer, M., Bhagavan, S., Smith, B.H., and Laurent, G. (1997). Impaired odor discrimination on desynchronization of odor-encoding neural assemblies. Nature *390*, 70–74.

Storm, J.F. (1990). Potassium currents in hippocampal pyramidal cells. Prog. Brain Res. *83*, 161–187.

Stryker, M.P. (1989). Cortical physiology: is grandmother an oscillation? Nature *338*, 297–298.

Stuart, G., and Sakmann, B. (1995). Amplification of EPSPs by axosomatic sodium channels in neocortical pyramidal neurons. Neuron *15*, 1065–1076.

Suzuki, S., and Cavanagh, P. (1995). Facial organization blocks access to low-level features: an object inferiority effect. J. Exp. Psychol. Hum. Percept. Perform. *21*, 901–913.

Szentagothai, J. (1973). Synaptology of the visual cortex. In Handbook of Sensory Physiology VII/3B: Visual Centers in the Brain, R. Jung, ed. (New York: Springer-Verlag).

Tallon-Baudry, C., and Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. Trends Cogn. Sci. *3*, 151–162.

Tallon-Baudry, C., Bertrand, O., Delpuech, C., and Pernier, J. (1996). Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. J. Neurosci. *16*, 4240–4249.

Tallon-Baudry, C., Bertrand, O., Delpuech, C., and Pernier, J. (1997). Oscillatory gamma band (30–70 Hz) activity induced by a visual search task in humans. J. Neurosci. *17*, 722–734.

Tallon-Baudry, C., Bertrand, O., Peronnet, F., and Pernier, J. (1998). Induced gamma band activity during the delay of a visual short-term memory task in humans. J. Neurosci. *18*, 4244–4254.

Tallon-Baudry, C., Kreiter, A.K., and Bertrand, O. (1999). Sustained and transient oscillatory responses in the gamma and beta bands in a visual short-term memory task in humans. Vis. Neurosci., in press.

Tanaka, K. (1993). Neuronal mechanisms of object recognition. Science *262*, 685–688.

Tanaka, K. (1996). Inferotemporal cortex and object vision: stimulus selectivity and columnar organization. Annu. Rev. Neurosci. *19*, 109–139.

Tanaka, K., and Saito, H.-A. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. J. Neurophysiol. *62*, 626–641.

Tanaka, K., Hikosaka, K., Saito, H., Yukie, M., Fukada, Y., and Iwai, E. (1986a). Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. J. Neurosci. *6*, 134–144.

Tanaka, M., Weber, H., and Creutzfeldt, O.D. (1986b). Visual properties and spatial distribution of neurones in the visual association area on the prelunate gyrus of the awake monkey. Exp. Brain. Res. *65*, 11–37.

Tanaka, K., Fukada, Y., and Saito, H.A. (1989). Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the macaque monkey. J. Neurophysiol. *62*, 642–656.

Tarr, M.J., and Bulthoff, H.H. (1995). Is human object recognition better described by geon-structural-descriptions or by multiple-views? J. Exp. Psychol. Hum. Percept. Perform., in press.

Theeuwes, J., and Kooi, J.L. (1994). Parallel search for a conjunction of shape and contrast polarity. Vision Res. *34*, 3013–3016.

Thomson, A.M., and Deuchars, J. (1997). Synaptic interactions in neocortical local circuits: dual intracellular recordings in vitro. Cereb. Cortex *7*, 510–522.

Thomson, A.M., and West, D.C. (1993). Fluctuations in pyramidal-pyramidal excitatory postsynaptic potentials modified by presynaptic firing pattern and postsynaptic membrane potential using paired intracellular recordings in rat neocortex. Neuroscience *54*, 329–346.

Thomson, A., Deuchars, J., and West, D. (1993). Single axon excitatory postsynaptic potentials in neocortical interneurons exhibit pronounce paired pulse facilitation. Neuroscience *54*, 347–360.

Thorpe, S., Fize, D., and Marlot, C. (1996). Speed of processing in the human visual system. Nature *381*, 520–522.

Tiitinen, H., Sinkkonen, J., Reinikainen, K., Alho, K., Lavikainen, J., and Naatanen, R. (1993). Selective attention enhances the auditory 40-Hz transient response in humans. Nature *364*, 59–60.

Tipper, S.P., Weaver, B., Jerreat, L.M., and Burak, A.L. (1994). Object-based and environment-based inhibition of return of visual attention. J. Exp. Psychol. Hum. Percept. Perform. *20*, 478–499.

Tipper, S.P., and Weaver, B. (1998). The medium of attention: location-based, object-based, or scene-based? In Visual Attention, Volume 8, R.D. Wright, ed. (Oxford: Oxford University Press).

Tong, F., Nakayama, K., Vaughan, J.T., and Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. Neuron *21*, 753–759.

Tononi, G., and Edelman, G.M. (1998). Consciousness and complexity. Science *282*, 1846–1851.

Tononi, G., Sporns, O., and Edelman, G. (1992). Reentry and the problem of integrating multiple cortical areas: simulation of dynamic integration in the visual system. Cereb. Cortex *2*, 310–335.

Tononi, G., Srinivasan, R., Russell, D.P., and Edelman, G.M. (1998). Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. Proc. Natl. Acad. Sci. USA *95*, 3198–3203.

Tootell, R.B.H., and Hamilton, S.L. (1989). Functional anatomy of the second visual area (V2) in the macaque. J. Neurosci. *9*, 2620–2644.

Tootell, R.B.H., and Taylor, J.B. (1995). Anatomical evidence for MT and additional cortical visual areas in humans. Cereb. Cortex *1*, 39–55.

Tootell, R.B.H., Dale, A.M., Sereno, M.I., and Malach, R. (1996). New images from human visual cortex. Trends Neurosci. *19*, 481–489.

Tovee, M., and Rolls, E. (1992a). Oscillatory activity is not evident in the primate temporal visual cortex with static stimuli. Neuroreport *3*, 369–372.

Tovee, M.J., and Rolls, E.T. (1992b). The functional nature of neuronal oscillations. Trends Neurosci. *15*, 387.

Toyama, K., Kimura, M., and Tanaka, K. (1981a). Cross-correlation analysis of interneuronal connectivity in cat visual cortex. J. Neurophysiol. *46*, 191–201.

Toyama, K., Kimura, M., and Tanaka, K. (1981b). Organization of cat visual cortex as investigated by cross-correlation techniques. J. Neurophysiol. *46*, 202–214.

Traub, R.D., Wong, R.K.S., Miles, R., and Michelson, H.B. (1991). A model of a CA3 hippocampal pyramidal neuron incorporating voltage-clamp data on intrinsic conductances. J. Neurophysiol. *66*, 635–650.

Traub, R.D., Whittington, M.A., Stanford, I.M., and Jefferys, J.G. (1996). A mechanism for generation of long-range synchronous fast oscillations in the cortex. Nature *383*, 621–624.

Treisman, A. (1982). Perceptual grouping and attention in visual search for features and for objects. J. Exp. Psychol. Hum. Percept. Perform. *8*, 194–214.

Treisman, A. (1988). Features and objects: the fourteenth Bartlett memorial lecture. Quart. J. Exp. Psychol. *40A*, 201–237.

Treisman, A. (1991). Search, similarity and the integration of features between and within dimensions. J. Exp. Psychol. Hum. Percept. Perform. *27*, 652–676.

Treisman, A. (1992a). Perceiving and reperceiving objects. Am. Psychol. *47*, 862–875.

Treisman, A. (1992b). Spreading suppression or feature integration? A reply to Duncan and Humphreys. J. Exp. Psychol. Hum. Percept. Perform. *18*, 589–593.

Treisman, A. (1993). The perception of features and objects. In Attention: Selection, Awareness and Control: A Tribute to Donald Broadbent, A. Baddeley and L. Weiskrantz, eds. (Oxford: Clarendon Press).

Triesman, A. (1995). Modularity and attention: is the binding problem real? Vis. Cogn. *2*, 303–311.

Treisman, A. (1996). The binding problem. Curr. Opin. Neurobiol. *6*, 171–178.

Treisman, A. (1998). Feature binding, attention and object perception. Philos. Trans. R. Soc. Lond. B Biol. Sci. *353*, 1295–1306.

Treisman, A., and Gelade, G. (1980). A feature-integration theory of attention. Cogn. Psychol. *12*, 97–136.

Treisman, A., and Gormican, S. (1988). Feature analysis in early vision: evidence from search asymmetries. Psychol. Rev. *95*, 15–48.

Treisman, A., and Kanwisher, N.K. (1998). Perceiving visually-presented objects: recognition, awareness, and modularity. Curr. Opin. Neurobiol. *8*, 218–226.

Treisman, A., and Sato, S. (1990). Conjunction search revisited. J. Exp. Psychol. Hum. Percept. Perform. *16*, 459–478.

Treisman, A., and Schmidt, H. (1982). Illusory conjunctions in the perception of objects. Cogn. Psychol. *14*, 107–141.

Treisman, A., and Souther, J. (1986). Illusory words: the roles of attention and of top-down constraints in conjoining letters to form words. J. Exp. Psychol. Hum. Percept. Perform. *12*, 3–17.

Treue, S., and Andersen, R.A. (1996). Neural responses to velocity gradients in macaque cortical area MT. Vis. Neurosci. *13*, 797–804.

Treue, S., and Maunsell, J.H.R. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. Nature *382*, 539–541.

Triesch, J., and von der Malsburg, C. (1996). Binding—a proposed experiment and a model. In Proceedings of the Proceedings of the International Conference on Artificial Neural Networks 1996 (New York: Springer-Verlag).

Tsal, Y. (1989). Do illusory conjunctions support feature integration theory? A critical review of theory and findings. J. Exp. Psychol. Hum. Percept. Perform. *15*, 394–400.

Ts'o, D., and Gilbert, C. (1988). The organization of chromatic and spatial interactions in the primate striate cortex. J. Neurosci. *8*, 1712–1727.

Ts'o, D.Y., Gilbert, C.D., and Wiesel, T.N. (1986). Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis. J. Neurosci. *6*, 1160–1170.

Tsotsos, J.K. (1990). Analyzing vision at the complexity level. Behav. Brain Sci. *13*, 423–445.

Tsotsos, J.K. (1995). Toward a computational model of visual attention. In Early Vision and Beyond, T.V. Papathomas, ed. (Cambridge, MA: MIT Press).

Tsotsos, J.K., Culhane, S.N., Wai, W.Y.K., Lai, Y., Davis, N., and Nuflo, F. (1995). Modeling visual attention via selective tuning. Artif. Intell. *78*, 507–545.

Ullman, S. (1996). High-Level Vision (Cambridge, MA: MIT Press).

Ungerleider, L., and Haxby, J. (1994). "What" and "Where" in the human brain. Curr. Opin. Neurobiol. *4*, 157–165.

Ungerleider, L.G., and Mishkin, M. (1982). Two cortical visual systems. In Analysis of Visual Behavior, D.J. Ingle, M.A. Goodale, and R.J.W. Mansfield, eds. (Cambridge, MA: MIT Press).

Ungerleider, L.G., Gaffan, D., and Pelak, V.S. (1989). Projections from inferior temporal cortex to prefrontal cortex via the uncinate fascicle in rhesus monkeys. Exp. Brain Res. *76*, 473–484.

Usher, M., and Donnelly, N. (1998). Visual synchrony affects binding and segmentation in perception. Nature *394*, 179–182.

Usrey, W.M., and Reid, R.C. (1999). Synchronous activity in the visual system. Annu. Rev. Physiol. *61*, 435–456.

Vaadia, E., and Aertsen, A. (1992). Coding and computation in the cortex: single-neuron activity and cooperative phenomena. In Information Processing in the Cortex: Experiments and Theory, A. Aertsen and V. Braitenberg, eds. (New York: Springer-Verlag).

Vaadia, E., Ahissar, E., Bergman, H., and Lavner, Y. (1991). Correlated activity of neurons: a neural code for higher brain functions? In Neuronal Cooperativity, J. Kruger, ed. (Berlin: Springer-Verlag).

Vaadia, E., Haalman, I., Abeles, M., Bergman, H., Prut, Y., Slovin, H., and Aertsen, A. (1995). Dynamics of neuronal interactions in monkey cortex in relation to behavioural events. Nature *373*, 515–518.

Van Essen, D.C., and Anderson, C.H. (1990). Information processing strategies and pathways in the primate retina and visual cortex. In An Introduction to Neural and Electronic Networks, S.F. Zornetzer, J.L. Davis, and C. Lau, eds. (New York: Academic Press).

Van Essen, D.C., and Gallant, J.L. (1994). Neural mechanisms of form and motion processing in the primate visual system. Neuron *13*, 1–10.

Van Essen, D.C., and Zeki, S.M. (1978). The topographic organization of rhesus monkey prestriate cortex. J. Physiol. (Lond.) *277*, 193–226.

Van Essen, D.C., Anderson, C.H., and Felleman, D.J. (1992). Information processing in the primate visual system: an integrated systems perspective. Science *255*, 419–423.

van Vreeswijk, D., Abbott, L.F., and Ermentrout, G.B. (1994). When inhibition not excitation synchronizes neural firing. J. Comput. Neurosci. *1*, 313–321.

Varela, F.J. (1995). Resonant cell assemblies: a new approach to cognitive functions and neuronal synchrony. Biol. Res. *28*, 81–95.

Vecera, S.P., and Farah, M.J. (1994). Does visual attention select objects or locations? J. Exp. Psychol. Gen. *123*, 146–160.

Vogels, R., and Orban, G.A. (1994). Activity of inferior temporal neurons during orientation discrimination with successively presented gratings. J. Neurophysiol. *71*, 1428–1451.

Volgushev, M., Chistiakova, M., and Singer, W. (1998). Modification of discharge patterns of neocortical neurons by induced oscillations of the membrane potential. Neuroscience *83*, 15–25.

von der Heydt, R., and Dursteler, M.R. (1993). Visual search: monkeys detect conjunctions as fast as features. Invest. Ophthalmol. Vis. Sci. *34*, 1288.

von der Malsburg, C. (1981). The correlation theory of brain function. MPI Biophysical Chemistry, Internal Report 81–2. Reprinted in Models of Neural Networks II (1994), E. Domany, J.L. van Hemmen, and K. Schulten, eds. (Berlin: Springer).

von der Malsburg, C. (1985). Nervous structures with dynamical links. Ber. Bunsenges. Phys. Chem. *89*, 703–710.

von der Malsburg, C. (1986). Am I thinking assemblies? In Proceedings of the Trieste Meeting on Brain Theory, G. Palm and A. Aertsen, eds. (Springer: Berlin).

von der Malsburg, C. (1988). Pattern recognition by labeled graph matching. Neural Networks *1*, 141–148.

von der Malsburg, C. (1995). Binding in models of perception and brain function. Curr. Opin. Neurobiol. *5*, 520–526.

von der Malsburg, C. (1999). The what and why of binding: the modeler's perspective. Neuron *24*, this issue, 95–104.

von der Malsburg, C., and Bienenstock, E. (1987). A neural network for the retrieval of superimposed connection patterns. Europhys. Lett. *3*, 1243–1249.

von der Malsburg, C., and Buhmann, J. (1992). Sensory segmentation with coupled neural oscillators. Biol. Cybern. *67*, 233–242.

von der Malsburg, C., and Reiser, K. (1995). Pose invariant object recognition in a neural system. In Proceedings of the International Conference on Artificial Neural Networks 1995, F. Fogelman-Souli, J.C. Rault, P. Gallinari, and G. Dreyfus, eds. (New York: Springer-Verlag).

von der Malsburg, C., and Schneider, W. (1986). A neural cocktail-party processor. Biol. Cybern. *54*, 29–40.

von der Malsburg, C., and Singer, W. (1991). Principles of cortical network organization. In Neurobiology of Neocortex, P. Rakic and W. Singer, eds. (New York: John Wiley).

von Helmholtz, H.L.F. (1925). Treatise on Physiological Optics (New York: Dover Press).

Wallis, G., and Rolls, E. (1997). A model of invariant object recognition in the visual system. Prog. Neurobiol. *51*, 167–294.

Wandell, B.A. (1999). Computational neuroimaging of human visual cortex. Annu. Rev. Neurosci. *22*, 145–173.

Wang, X.-J. (1999). Fast burst firing and short-term synaptic plasticity: a model of neocortical chattering neurons. Neuroscience *89*, 347–362.

Wang, X.-J., and Buzsaki, G. (1996). Gamma oscillation by synaptic inhibition in a hippocampal interneuronal network model. J. Neurosci. *16*, 6402–6413.

Wang, D.L., Buhmann, J., and von der Malsburg, C. (1990). Pattern segmentation in associative memory. Neural Comput. *2*, 94–106.

Wang, Q., Cavanagh, P., and Green, M. (1994). Familiarity and pop-out in visual search. Percept. Psychophys. *56*, 495–500.

Wehr, M., and Laurent, G. (1996). Odour encoding by temporal sequences of firing in oscillating neural assemblies. Nature *384*, 162–166.

Weisstein, N. (1973). Beyond the yellow Volkswagen detector and the grandmother cell: a general strategy for the exploration of operations in human pattern recognition. In Contemporary Issues in Cognitive Psychology: The Loyola Symposium, R.L. Solso, ed. (Washington, DC: Winston/Wiley).

Wertheimer, M. (1923). Untersunchungen zur Lehre der Gestalt. Psychol. Forschung *4*, 301–350.

Wertheimer, M. (1955). Laws of organization in perceptual forms. In A Source Book of Gestalt Psychology, W.D. Ellis, ed. (London: Routledge and Kegan Paul).

Wespatat, V., Tennigkeit, F., and Singer, W. (1999). Oscillations and long-term synaptic plasticity in rat visual cortex. In From Molecular Neurobiology to Clinical Neuroscience: Proceedings of the 1st Göttingen Conference of the German Neuroscience Society, Volume 1, 27th Göttingen Neurobiology Conference, N. Elsner and U. Eysel, eds. (Stuttgart: Thieme-Verlag).

Whittington, M.A., Traub, R.D., and Jefferys, J.G.R. (1995). Synchronized oscillations in interneuron networks driven by metabotropic glutamate receptor activation. Nature *373*, 612–615.

Wickelgren, W. (1969). Context-sensitive coding, associative memory, and serial order in (speech) behavior. Psychol. Rev. *76*, 1–15.

Wilson, M., and Bower, J.M. (1992). Cortical oscillations and temporal interactions in a computer simulation of piriform cortex. J. Neurophysiol. *67*, 981–995.

Wilson, M.A., and McNaughton, B.L. (1993). Dynamics of the hippocampal ensemble code for space. Science *261*, 1055–1058.

Wilson, F.A., Scalaidhe, S.P., and Goldman-Rakic, P.S. (1993). Dissociation of object and spatial processing domains in primate prefrontal cortex. Science *260*, 1955–1958.

Wiskott, L. (1999). The role of topographical constraints in face recognition. Pattern Recog. Lett. *20*, 89–96.

Wiskott, L., and von der Malsburg, C. (1995). Face recognition by dynamic link matching. In Lateral Interactions in the Cortex: Structure and Function (electronic book), J. Sirosh, R. Miikkulainen, and Y. Choe, eds., www.cs.utexas.edu/users/nn/web-pubs/htmlbook96.

Wolfe, J.M. (1992). "Effortless" texture segmentation and "parallel" visual search are not the same thing. Vision Res. *32*, 757–763.

Wolfe, J.M. (1994a). Guided Search 2.0: a revised model of visual search. Psychon. Bull. Rev. *1*, 202–238.

Wolfe, J.M. (1994b). Visual search in continuous, naturalistic stimuli. Invest. Opthalmol. Visu. Sci. *35*, 13–28.

Wolfe, J.M. (1996). Extending Guided Search: why Guided Search needs a preattentive "item map." In Converging Operations in the Study of Visual Selective Attention, A. Kramer, G.H. Cole, and G.D. Logan, eds. (Washington, DC: American Psychological Association).

Wolfe, J.M. (1998). What do 1,000,000 trials tell us about visual search? Psychol. Sci. *9*, 33–39.

Wolfe, J., and Bennett, S. (1996). Preattentive object files: shapeless bundles of basic features. Vision Res. *37*, 25–44.

Wolfe, J.M., and Cave, K.R. (1999). The psychophysical evidence for a binding problem in human vision. Neuron *24*, this issue, 11–17.

Wolfe, J.M., and Gancarz, G. (1996). Guided Search 3.0: a model of visual search catches up with Jay Enoch 40 years later. In Basic and Clinical Applications of Vision Science, V. Lakshminarayanan, ed. (Dordrecht, Netherlands: Kluwer Academic).

Wolfe, J.M., Cave, K.R., and Franzel, S.L. (1989). Guided Search: an alternative to the Feature Integration model for visual search. J. Exp. Psychol. Hum. Percept. Perform. *15*, 419–433.

Wolfe, J.M., Chun, M.M., and Friedman-Hill, S.R. (1995). Making use of text on gradients: visual search and perceptual grouping exploit the same parallel processes in different ways. In Early Vision and Beyond. T. Papathomas, C. Chubb, A. Gorea, and E. Kowler, eds. (Cambridge, MA: MIT Press).

Würtz, R. (1997). Object recognition robust under translations, deformations, and changes in background. IEEE Trans. Pattern Anal. Machine Intell. *19*.

Yantis, S., and Gibson, B.S. (1994). Object continuity in apparent motion and attention. Can. J. Exp. Psychol. *48*, 182–204.

Yen, S.-C., and Finkel, L.H. (1998). Extraction of perceptually salient contours by striate cortical networks. Vision Res. *38*, 719–741.

Yen, S.-C., Menschik, E.D., and Finkel, L.H. (1999). Perceptual grouping in striate cortical networks mediated by synchronization and desynchronization. Neurocomputing, in press.

Yeshurun, Y., and Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. Nature *396*, 72–75.

Yeshurun, Y., and Carrasco, M. (1999). Spatial attention improves performance in spatial resolution tasks. Vision Res. *39*, 293–306.

Ylinen, A., Sik, A., Bragin, A., Nadasdy, Z., Jando, G., Szabo, I., and Buzsaki, G. (1995). Sharp wave-associated high-frequency oscillation (200 Hz). in the intact hippocampus: network and intracellular mechanisms. J. Neurosci. *15*, 30–46.

Yoshioka, T., Blasdel, G.G., Levitt, J.B., and Lund, J.S. (1996). Relation between patterns of intrinsic lateral connectivity, ocular dominance, and cytochrome oxidase-reactive regions in macaque monkey striate cortex. Cereb. Cortex *6*, 297–310.

Young, M.P., and Yamane, S. (1992). Sparse population coding of faces in the inferotemporal cortex. Science *256*, 1327–1331.

Young, M.P., Tanaka, K., Yamane, S. (1992). On oscillating neuronal responses in the visual cortex of the monkey. J. Neurophysiol. *67*, 1464–1474.

Yu, A.C., and Margoliash, D. (1996). Temporal hierarchical control of singing in birds. Science *273*, 1871–1875.

Yuste, R., and Tank, D.W. (1996). Dendritic integration in mammalian neurons, a century after Cajal. Neuron *16*, 701–716.

Zeki, S.M. (1978). Functional specialisation in the visual cortex of the rhesus monkey. Nature *274*, 423–428.

Zeki, S. (1983). The distribution of wavelength and orientation selective cells in different areas of monkey visual cortex. Proc. R. Soc. Lond. B Biol. Sci. *217*, 449–470.

Zeki, S., and Shipp, S. (1988). The functional logic of cortical connections. Nature *335*, 311–317.

Zhang, X. (1999). Anticipatory inhibition: an intentional non-spatial mechanism revealed with the distractor previewing technique. PhD thesis, Princeton University, Princeton, NJ.

Zhang, L.I., Tao, H.W., Holt, C.E., Harris, W.A., and Poo, M. (1998). A critical window for cooperation and competition among developing retinotectal synapses. Nature *395*, 37–44.

Zipser, K., Lamme, V.A.F., and Schiller, P.H. (1996). Contextual Modulation in Primary Visual Cortex. J. Neurosci. *16*, 7376–7389.

Zohary, E., and Hochstein, S. (1989). How serial is serial processing in vision? Perception *18*, 191–200.

Zohary, E., Shadlen, M.N., and Newsome, W.T. (1994). Correlated neuronal discharge rate and its implications for psychophysical performance. Nature *370*, 140–143.